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Greetings to Ambrus Ábrahám on the occasion of his 81st birthday

At a joint ceremonial meeting on 22 November, 1973 the Szeged Comittees of the Hungarian Biological Society and the Hungarian Academy of Sciences, and the Biological Comittee of Attila József University greeted Academician Ambrus Ábrahám, Professor Emeritus of Attila József University, on the occasion of his 81st birthday. The meeting was attended by representatives of the Hungarian Academy of Sciences, Attila József University and the Teacher's Training College, together with the professor's students, admirers and friends. Speeches of greeting were made by J. MEGYERI, G. FODOR and I. HORVÁTH.

Dr. JÁNOS MEGYERI, lecturer at the Szeged Teachers' Training College, made the following address:

"In the name of the directorate and members of the Hungarian Biological Society, and also of his one-time students, it is with respect and pleasure that I greet the 80-year-old Academician ÁBRAHÁM, one of the founder members of our Society, its ex-president, and an honorary member, our professor and master.

I greet him with esteem on this pleasant occasion, here in this well-remembered place, this lecture room of this institute, where he created, trained his students to love science, and stimulated them as a lecturing professor and as chairman of the lecturing sessions of our society.

We greet our professor with respect and pride. With respect because his life and work have encouraged and continue to encourage respect and high esteem in everyone who has come to know him.

In what way? By his knowledge and will-power, with which he always served the common good. We respect him because he was resolute, and did not recognize obstacles in the achievement of a good and useful aim. We respect him because he scorned and did not esteem the moaners, who considered only the difficulties, but hardly did anything, in his own frequently-used expression the "cunctators".

We respect Academician ÁBRAHÁM, for he has always applied unfaltering will-power to that work which is often tiring, which often appears dull, and which apart from intuitive recognition demands much endurance. This is scientific work: that work which is one of the most wonderful of human activities, which is a source of human prosperity and progress, which helps us to recognize ourselves, which lifts aside the veil concealing the secrets and laws of nature, and the results of which promote practical work, arm man against the forces of nature, and provide man with pleasure, with the prosperity desired in some form by all mankind, and rarely with happiness too.

His respect-demanding life and work are none other in our eyes than the fulfilment of a wonderful programme:

to research, to struggle and not to retreat.

He carried out research, and thus had a part in what is known as human struggle. He too was affected by certain forces, when many other men retreated. Academician ÁBRAHÁM did not retreat, but faced the difficulties as the slender pines of his homeland weather the storms.

In September 1917, as a third-year university student and at the time as a temporary assistant lecturer he first stepped to a teaching-desk and first stood before young people desiring to learn; he simultaneously began his research work and to report the acquired knowledge.

For nearly 50 years he stood before his students and delivered his lectures clearly, understandably, colourfully and in fine language, with imposing knowledge and without any artificial methods.

We saw that for him the institute and the teaching meant pleasure. It was here, in the teaching room and the institute, that he lived, enthused and inspired. It was here that he materialized as a full man, who knew how to be merry and how to produce a cheerful atmosphere while lecturing on problems requiring the most intense attention, in order that the good humour should freshen the students. We who were able to work in his institute were unable to decide where our professor enjoyed himself most, beside his microscope in the laboratory, or in the lecturing room. We now know that he felt equally at home in both places. We now see that Academician ÁBRAHÁM's life put into practice the conception of the unity of research, teaching and pedagogy at a time when it was not yet fashionable to talk of this as a fundamental principle of higher education.

In his workplaces at the Budapest University, from 1934 at the Teachers' Training College in Szeged, and from 1940 at the Szeged University, his work was the perfect realization of the unity of laboratory and lecturing room, of research and teaching.

The realization of this unity and of this principle of constant and undiminished intensity gave birth to his usually rich scientific results, and shaped and formed

his many, well-trained students to the respect of science, to the teaching of true knowledge, and to the love above all of the homeland.

Hundreds of his students in the most varied teaching positions (from primary schools to universities), and in research institutes throughout the country are now carrying out their work as they saw it performed by their professor, and as he advised: "Always look for and teach the true, the verified and the science. Teach by example, and not by eloquence, for intelligent teaching is possible only by example."

His research results of many decades on his scientific theme, the nervous system, the most beautiful and most complex structure, passed far beyond the borders of the whole scientific world.

The name of Academician ÁBRAHÁM was made known, recognized and respected throughout the world by more than 260 papers and a large series of independently written books and monographs. As a result of his work aimed at elucidating the fine structure of the nervous system, his name is justifiably mentioned with the same respect as the names of Camillo Golgi and Ramon y Cajal; and what is more important, his research results help the work of the physician, the psychologist and the biologist striving to clarify the numerous unsolved mysteries of life.

On thumbing through his papers and books, one understands just how much he worked, and why he is still working today with undiminished enthusiasm: for the public good, taken in the broadest sense, which should be served directly or indirectly by science.

It is with pride that we greet our 80-year-old master, and I should like to take this opportunity of expressing our thanks and gratitude to him.

We thank you, Professor, for our pride in you, and for our ability to proclaim ourselves your students.

We are filled with pride and pleasure that you too have played your part in the fact that our country and the name of Hungary is recognized abroad. We greet you, Academician ÁBRAHÁM, on the basis of the results of your work a member of many top-ranking foreign scientific societies, a lecturer at numerous conferences, and a consultant of a large number of research institutes and university departments. Not only have you travelled the world, to report the results of your constructive genius to other experts, but many have come, and still come to your laboratory to learn from you.

Your students remember with pride that in the great cities of India, Europe and America Academician ÁBRAHÁM did just the same as in his university department: he was not only a scholar reporting his results to the scientific world, but, whether speaking English or German, remained a Hungarian, dearly loving his countrymen and always ready to serve the interests of the Hungarian people. We are also proud that you trained us too to this, and again express our gratitude and respect to you.

Finally, in the name of the Hungarian Biological Society, your ex-students and the one-time colleagues of your department, let me express the sincere wish that you work long in good health for the progress of Hungarian and universal science. May your great plans and aims materialize, and may you partake in much pleasure and honour; although you never sought for and expected this latter, if you did receive it you were pleased, and still are pleased, because you are a man, and because one of man's perpetual needs is pleasure caused by the good and the beautiful.

Let us wish that you may work and create for a very long time to come, for I know that one of the principles of your life is this. As Billroth put it: "Without creation and work, life is not worth even one breath...".

Create and work, therefore, and long may you live!"

DR. GÉZA FODOR, Rector of the University, then made the following address: "It is with very great pleasure that I greet Professor AMBRUS ÁBRAHÁM in the name of the leadership of Attila József University, on the occasion of his 81st birthday, when the Presidium of the Hungarian People's Republic has awarded him the Order of Labour, Gold Grade. I wish you long life, strength, health and every success in your future work.

Unfortunately, Deputy-Minister KÁROLY POLINSYKY is otherwise engaged, and is unable to attend this ceremony to make the award, and thus the task has fallen to me to read out and pass on to the Professor the letter of Dr. MIKLÓS NAGY Minister of Education: "Dear Professor, allow me to add my name to the list of, those greeting you on the occasion of your 81st birthday, in recognition of your outstanding scientific activity, your teaching work at the university over three decades, and your personal attitude. I greet you most warmly.

I hope that you will continue for many years to increase still further your authority both in Hungary and abroad, and to serve the interests of our socialist homeland with your activity. At this time I should like to inform you that on this occasion the Presidium of the Hungarian People's Republic has awarded you the Order of Labour, Gold Grade.

Please accept my sincere congratulations and good wishes."

Again I wish you long life, strength, health and every success in your work."

The next speaker was Professor Dr. IMRE HORVÁTH, Chairman of the University Biological Committee, who spoke as follows: "In the name of the Biological Committee I greet Academician AMBRUS ÁBRAHÁM with respect and affection on the occasion of his 81st birthday, and wish that long may he work and create in our midst.

Reference has already been made at this ceremonial meeting to personal experiences, and I too should like to do this. In recent years we have been dealing increasingly with questions of teaching and educational work. Looking back on my university years, I frequently think of Professor ÁBRAHÁM's lectures. These always meant an experience to me, and as regards their form and content each was a work of art. Professor ÁBRAHÁM frequently recounted to us students that he attached great importance to the university lectures; even as an elderly professor, he would spend 4—5 hours preparing for each lesson. I do not know whether every university lecturer can say today that he has prepared conscientiously always for his lectures and practicals. I am afraid that we perhaps speak more of the educational work than we actually do towards it, not least of all with our individual examples. I respect Professor ÁBRAHÁM as a world-famous scholar, but I respect him particularly as a university teacher.

Again I wish you, Professor ÁBRAHÁM, strength, health and a long life rich in creative work. I wish that you will be the example for an ever greater number of university lecturers."

Greeting addresses were also made by Dr. JÁNOS SZENTÁGOTHAI, Professor of the Semmelweis Medical University, Budapest, Vice-Chairman of the Hungarian Academy of Sciences; Dr. JÁNOS BALOGH, Professor of Loránd Eötvös University, Chairman of the Biological Division of the Hungarian Academy of Sciences; Dr.

FERENC MÁRTA, Prorector of Attila József University; and Dr. LÁSZLÓ LEINDLER, Dean of the Faculty of Science József Attila University. Two students next greeted the Professor with bouquets of flowers.

After the conclusion of the ceremonial greetings Professor ÁBRAHÁM expressed his thanks to the Presidium of the Hungarian People's Republic for the second award of the Order of Labour, Gold Grade. He also expressed his thanks for the greetings, and then read out telegrams of congratulations from the Chairman and General Secretary of the Hungarian Academy of Sciences, and friends from London, Sofia and Tokyo. He further expressed his thanks to those present, and to all those who, on the occasion of the completion of his 80th year, had sent their good wishes in such a multitude of telegrams and letters.

Scientific curriculum of Dr. Ambrus Ábrahám

Dr. Ambrus Ábrahám, retired Professor of Attila József University, Szeged, Member of the Hungarian Academy of Sciences, holder of the Kossuth Prize (1953), was born at Tusnád in the county of Csik on 20 November 1893. He attended primary school at Tusnád, and grammar schools at Csiksomlyó and Csikszereda. In 1915 he was enrolled into the geography and biology in the Faculty of Philosophy at Budapest University. In 1919 he received his secondary-school teaching diploma, and in 1922 his doctoral diploma, with zoology as main subject, and botany and geology as subsidiary subjects. In 1917, as a third-year university student, he was chosen as assistant lecturer in the Department of General Zoology and Comparative Anatomy and Histology at the University. In the same Department he later became a fully accredited assistant lecturer and lecturer. In 1926 he was docent in "Histology of the Vertebrates", and in 1936 became associate professor. In 1934 he was appointed Professor of Zoology at the State Teachers' Training College in Szeged, and also leader of the Zoological Department. From August 1939 he was the Director of the same state Teachers' Training College. From November 1940 he was Professor of General Zoology and Comparative Anatomy in the Faculty of Science at Szeged University, and Director of the University Zoology and Biology Department. In 1946 he was elected a corresponding member of the Hungarian Academy of Sciences, and in 1960 ordinary member. He is an external member of the Royal Society of Medicine, a member of the Indian Academy of Zoology, the World Federation of Neurology and the Association of European Endocrinologists, and an honorary member of the Hungarian Biological Society and the Scientific Education Society. He is a member of the editorial comittees of Zeitschrift für mikr. anat. Forschung and Acta Zoologica Acad. Sci. Hungariae. His scientific research work began in 1916 when, as a second-year university student, he won a prize in a competition "Describe on the basis of independent studies the organism and multiplication of parasitic Infusoria in Hungarian frog species". In this paper he gave the description of the parasitic Infusoria *(Opalina dimidiata, O. ranarum, O. obtrigona, O. similis Zelleri, Anoplophria intesitnalis, Balantidium coli* and *Nyctothereus faba)* in *Rana ridibunda, Bufo vulgaris, B. viridis, Hyla arborea, Bombinator pachypus* and *B. igneus*. When he was appointed an assistant lecturer in the General Zoology and Comparative Anatomy and Histology Department of the University as a third-year student, his interest turned to comparative histology, and before long to the nervous system. His scientific activity falls by and large into three parts: histology, hydrobiology and comparative neurohistology.

Even at the beginning of his research work he regarded histology only as a framework for him to be able to locate the nervous system in various tissuses, which he made the object of examination in the most varied organs of the most different animal species from practically the whole of the animal kingdom. In one of his histological papers he described blood vessels from the multilayered cuboidal epithelium of the bladder of the rabbit, while in another, which was his doctoral thesis, he used the most varied fixing and staining procedures to investigate the histological structure of the femoral glands of the Archaeo- and Neolacertae in *Lacerta viridis, L. agilis, L. muralis, L. taurica, L. muralis maltensis* and *L. horváthi.* After a careful description of the organism he discounts the conception that the femoral glands act as the holding organ in mating. In his view the femoral glands are odour organs connected with mating, in the sense that the residues of the glandular secretion let fall by the male serve as a pathfinder for the female. He observed differences in the structure and development of the femoral glands in the two large lizard groups (Archaeo- and Neolacertae).

He regarded the hydrobiological investigations as seasonal work. In the course of this work, together with his colleagues he examined the springs of the Mátra and the hills close to Budapest or the Danube bend, and carried out extensive studies relating to the incidence of the Planariae. On this basis, from the occurrence of *Planaria alpina* they were able to draw conclusions on the extent of glaciation. With his students he later carried out systematic examinations in the brooks, springs and standing waters of the Bükk Mountain.

His comparative neurohistological studies extended to all types of organ in the most different species from the animal kingdom. If we wish to give an account of these, we must consider in turn those organ systems in which he examined the structure of the nervous system, the course of the nerve fibres, and their end-connection areas, the synapses. Before this, however, it should be recalled just what difficulties had to be faced in dealing with this extremely great problem, while he received no guidance in this either at home or from abroad. ÁBRAHÁM completed his university studies, and continued the comparative histology practicals for many years without ever having seen a single nerve cell or nerve fibre. For many long days and nights meditating at the laboratory table and leanding over the lenses of his microscopes, he himself had to find by experiment those methods which would reveal the nerve cells and the conducting and terminal systems consisting of the tremendous plexus of the processes of the nerve cells, the nerve fibres. But he succeeded. His unceasing work, endurance and steel-will were crowned with success. Following much and laborious work, he succeeded in developing methods which could overcome the problems awaiting solution, but not without difficulty, for this must be reckoned with everywhere and at all times by anyone having an interest in the structure and functioning of the nervous system. For us to be able to give a brief indication of this colossal activity, we must consider those organ systems on which ÁBRAHÁM carried out his neurohistological investigations, and to point out the results which he attained in the course of these.

When he had developed impregnating procedures suitable for the demonstration of the fine structures, he gladly devoted time to the intraepithelial fibres. Mainly of interest to him were the pathways of these, their connection to the epithelial cells and their termination. At present he is trying to acquire information with the electron-microscope as to whether there are synapses at the terminals of the intraepithelial nerve fibres running into the epithelia, and if so, then what the effect on

these is of the course of the keratinization in the keratinizing epithelia. Are they keratinized (which is probable), and if so, then are they re-formed? Are there intra-epithelial synapses, or not? He has carried out his examinations on the skin of man, the dog *(Canis familiaris)*, the elephant *(Elephas indicus)*, the mole *(Talpa europaea)*, the hedgehog *(Erinaceus europaeus)*, the green lizard *(Lacerta viridis)* and the mars frog *(Rana ridibunda)*. He has also followed the fate of the intraepithelial fibres in his investigations on lip cancer in humans, when he found that there are intact nerve fibres in the cancerous tissue.

As regards the organs of movement, he studied the nerve supply of the sphincter of *Anodonta cygnea* and established that the individual fibres of the nerve fibre plexuses end in terminal heads on the muscle fibres. He further reported that there are no nerve cells in the sphincter. He demonstrated the synapses in the oculomotor muscles of vertebrates, and followed the degeneration in frogs after the transsection of the nervus oculomotorius.

He demonstrated the sensory nerve terminal systems in the region of the gastro-intestinal system from the lips of humans, from the roots of moustache hairs, from the palate of the bear *(Ursus arctos)*, the rat *(Epimys rattus norvegicus)*, the dog *(Canis familiaris)* and hen *(Gallus domesticus)*, and from the palatine tonsils of humans. He described the receptor apparatus in the pre-stomach of birds *(Anas anas, Gallus domesticus)*, and proved that the nerve fibres supplying the smooth muscle cells end epicellularly in terminal heads. In the gastrointestinal tract of snails he showed that the terminal fibres of the nerve fibre plexuses interspersed with nerve cells end freely. Here he ran into the theories of ISTVÁN APÁTHY regarding continuity, and saw that the APÁTHY neurofibrils are nerve fibres which pass not through the body of the nerve cell, but below or above it. His research of the intestinal sections began with the bony fish *(Esox lucius, Tinca vulgaris)* and continued with the reptiles *(Emys orbicularis)* and the birds *(Gallus domesticus, Columba domestica, Anas, anas)*. He described intramural plexuses and nerve terminals in the smooth muscle tissue from all three origins.

He described nerve terminal organs of a sensory nature from the region of the breathing apparatus in the lung of lizards *(Lacerta agilis)*, and from the walls of the interalveolar septa, reported ganglia and nerve fibre plexuses in the lung of Emys orbicularis, pressoreceptors from the swimming-bladder of bony fish *(Cyprinus carpio, Carassius carassius)*, and characteristic intraepithelial fibres from the epiglottis of mammals *(Felis domestica)*.

The circulatory organ system is the region where ÁBRAHÁM worked much and where his name will perhaps be longest remembered in the annals of the international neurological literature. In his papers in this connection, which appeared in very great numbers, he deals with the nerve supply of the heart of fish, amphibia, reptiles, birds and mammals, including man. In a treatment extending to all parts of the heart and to every layer of the wall structure, he describes the nerve terminal organs of the myocardium, the intracardial ganglia,the interneuronal synapses and the receptors from the epicardium, the myocardium and the endocardium.

ÁBRAHÁM also carried out studies, similar in number and value to those on the heart, on the innervation of the vessels. Of these, which extend equally to the large vessels of birds, mammals and man, particular mention must be made of those referring to the tunica intima and the tunica media. As regards the former, in contrast to all opposing assertions he proved that it is free of nerve fibres. In the case of the latter he demonstrated that the nerve fibres entering the adventitia form a double

plexus: one of denser texture on the boundary of the adventitia and a looser one towards the intima. He showed that on the arcus aortae and the vena saphena the nerve fibres of the smooth muscle cells end in terminal heads.

His favourite objects were the coronary vessels, the arcus aortae and the sinus caroticus. From the first of these he reported nerve fibre plexuses and nerve terminal formations, the latter pointing to a receptor function in their structure. From the arcus aortae, which he studied in mammals *(Canis familiaris, Bos taurus, B. bubalus, Ovis aries)* in addition to humans, he described the terminal system of the aortic nerve and showed that, besides the considerable agreement in this, there are also significant differences. From a neurophysiological point of view too he reported an important structure from the arcus aortae of cattle, where the neurofibrillar end-plate layer is surrounded loop-like by a capillary, as proof that a neural end-plate of greater extent has greater oxygen and nutriment requirements. In his examinations of the many different forms of the sinus caroticus *(Homo, Canis familiaris, Ovis aries, Bos taurus, Sus scrofa domestica)*, he found that the end-plate systems exhibit more appreciable differences than those described from the arcus aortae.

The glomus caroticum, mainly of humans, is still a favourite research area of Professor ÁBRAHÁM today. Besides describing the structure, he demonstrated that the nerve fibres of vagal and glossopharyngeal origin end in terminal rings on the glomus cells. In his electron-microsopic examinations he found efferent synapses in the human glomus. In his view these remain unexplained if the glomus is considered exclusively as a chemoreceptor.

His results relating to the innervation of the vessels and to the heart have been published in monograph form. The work appeared first in German, and later, with a few variations and additions, in English.

He found the kidney of *Varanus griseus* most suitable for the demonstration of the nerve fibres of the renal tubules. On those tubule sections which can be regarded as ductus papillaris forms he demonstrated rich systems of nerve fibres and terminal plexuses, such as had never been observed in work related to the innervation of the kidney. As everyone else to date, ÁBRAHÁM was unable to detect the nerve supply of glomerulus but he could follow the nerve fibres up to the boundary of the glomerulus. He reported an almost unimaginable mass of nerve fibres from the larger arteries of the kidney (arteriae interlobares, arteriae interlobulares) and the wall of the renal pelvis in dog. In the dog kidney he could also follow the nerve fibres in the walls of the tubuli recti, and between the tubules found fibres which he classified as receptors. He detected receptors in the simple columnar epithelium lining the efferent tubules in the kidney of carp.

Among ÁBRAHÁM's neurohistological studies, a considerable place is occupied by the reproductive apparatus. His examinations were made on the penis of *Lacerta agilis, Epimys rattus, Felis domestica, Sus scrofa domestica, Bos taurus, Capra hircus*, and on the prepuce, glans penis and clitoris of humans. From the penis of the lizards he described simple intraepithelial fibres from the keratinizing stratified epithelium, which is covered in a special form towards the lumen by tapering keratinous squamae. The pictures which he reported on the receptors of the penis of mammals are so different, that from a single well-impregnated section it can be stated to which animal they pertain. Particularly characteristic are those relating to the prepuce and glans penis of humans. In the clitoris the complicated glomerulus systems predominate. They vary in position and number. Those lying directly below the epithelium are striking in form, richness and complexity.

Investigations relating to the central nervous system began on the nerve system of *Opisthodiscus diplodiscoides*, a parasitic trmeatode in the rectum of *Rana ridibunda*. These investigations provide information on the form of the system, and on the position and structure of its elements. The detailed account of the finer structures is given in those papers of ÁBRAHÁM describing the structure of the brain centres of *Dytiscus marginalis*, the synaptic connections of the visceral ganglion of *Aplysia california*, the philogenesis of the neurone, the mitosis of the cortical nerve cells of *Rana ridibunda*, and the giant synapses found in the motor nucleus of the nervus oculomotorius in *Cyprinus carpio*. An account of the structure of the cerebral cortex and the synapses is given by those studies carried out with an electron-microscope on the cerebral cortex of *Lacerta agilis*.

Research on the vegetative nervous system began with the human ganglion coeliacum. The interneuronal synapses were described, and among them a concentric plexus system which in a nest-like form encloses the body of the nerve cell. As regards the knowledge of the structure of the paravertebral ganglia, and mainly the synaptic connections, of particular importance are the comparative examinations carried out by ÁBRAHÁM on the ganglion stellatum and on the surgically removed paravertebral lumbal ganglia of patients with various vascular diseases. In the course of these, much evidence emerged that the terminal heads, the pericellular plexuses and other similar formations which at times appear en masse on the cells, are the terminals of the preganglionary fibres, and as such are interneuronal synapses. He distinguished two forms of these formations: a simpler one, and a more complicated one. In accordance with the Kirsche nomenclature, he classified the former as a synapsis with a low transmission surface, and the latter as a synapsis a high transmission surface.

In studies on the adrenal gland extending to all of the vertebrates higher than the fish, nerve cells nerve fibre plexuses and interneuronal synapses were described from the adrenal of *Rana ridibunda, Emys orbicularis, Columba domestica, Ardea cinerea, Rallus aquaticus* and *Fulica atra*. The adrenal medulla of mammals proved free of nerve cells possessing rich nerve fibre plexuses and terminal rings. He also performed electron-microscopic examinations on the adrenal of *Bufo viridis*. In these he made conclusions on the osmiophil and lipid cells, and also the summer cells, and described the transformation of the tubular mitochondria. He reported two axosomatic synapsis forms of the osmiophil cells, and established that there are Golgi bodies in the erythrocytes.

He dealt much with neurosecretion. He demonstrated that there are tremendous unipolar cells on both sides of the central line in the protocerebrum of *Dytiscus marginalis*. These produce masses of neurosecretion granules, which pass into the cranial nerves on intracerebral tracts consisting of neurites and crossing one another, and hence into the corpus cardiacum respectively corpus allatum. In addition to many publications describing his results in examinations with the light microscope, there are also others dealing with electron-microscope work.

In Professor ÁBRAHÁM's immense research work on neurohistology, virtually every form of sense organ was subjected to examination. A new sense organ was reported from the terrestrial Isopoda, and again from these animals he described the antennal receptors. He reported receptors from the antenna and uropodium of the Amphipoda, receptors and effectors from the gnathopodium, and receptors from the microscopic hairs covering the tergites. He described sense organs from

the antenna of *Trixalis nasuta*, and Johnston's organ from the antenna of *Diestrammena marmorata*. He reported receptors of the crista acustica and macula acustica from the membranaceous labyrinth of *Cyprinus carpio*. He described the synapses from the sclera and cornea of mammals, and the stratum gangliosum from the retina. He carried out electron-microscope studies of the retina of *Rana ridibunda* and Eimer's organ in *Talpa europaea*. On the above topics ÁBRAHÁM published more than 260 papers. These appeared in Állattani Közlemények, Studia Zoologica, Annales Biologici Universitatis Szegediensis, Annales Biologici Universitatum Hungariae, Magyar Tudományos Akadémia Biológiai Osztályközlemények, Orvostudományi Osztályközlemények, Akadémiai Matematikai és Természettudományi Értesítő, Acta Biologica Acad. Sci. Hung., Anatomischer Anzeiger, Morphologie und Oekologie der Tiere, Zellforschung und mikroskopische Anatomie, Mikroskopisch anatomische Forschung, Acta Anatomica, Zologischer Anzeiger Nature and the publications of various international symposia and congresses. The papers were reported in Zoologischer Bericht, Anatomischer Bericht, Berichte über die wissenschaftliche Biologie, Biological Abstracts and Excerpta Medica.

From both scientific and pedagogic aspects, the college and university lecture notes of Professor ÁBRAHÁM are of great value; these have been published in very different fields, in accordance with the requirements of the syllabus, under titles such as "General zoology, comparative anatomy, histology and physiology", "Zoophysiological anatomy", "Comparative Study of the Animal Organism", etc. Mention must also be made of his books, the first of which "Anatomy, physiology, hygienics", written jointly with his students, appeared in 1958; enlarged and in a somewhat different form, it was published again in 1971 under the title "Anatomy and physiology". In 1961 appeared his two-volume "Comparative Study of the Animal Organism" (1055 pages, 678 figures), in which he described the comparative functional anatomy of the animal kingdom. This work is a text-book for the university students.

In 1964 the Magyar Tudományos Akadémia published his monograph "Die mikroskopische Innervation des Herzens und der Blutgefässe von Vertebraten" (475 pages, with 217 original Figures). The work was very warmly received by the foreign reviewers. Very favourable reviews of the book were given by Berichte über die gesamte Biologie, Mikroskopie, Wiener Medicinische Wochenschrift, Zentralblatt für fie gesamte Neurologie und Psychiatrie, Biologisches Zentralblatt, L'Anné Biologique, etc. Extremely fine appreciations were expressed by letter by those to whom ÁBRAHÁM sent the monograph.

With a few additions and changes, the monograph appeared in English in 1969, under the title „Microscopic innervation of the heart and blood vessels in Vertebrates including man" (with 222 original figures), as a joint publication of the Magyar Tudományos Akadémia and Pergamon Press, Oxford. Forewords were written by C. Heimans, Professor of Pharmacology at the University of Ghent, a Nobel Prize winner, and by E. Neil, Professor of Physiology at the University of London. The work was rated highly by the specialists in this field.

Pictures from ÁBRAHÁM's neurohistological works were published by Adams in "The Comparative Morphology of the Carotid Sinus", and by Bullock and Horridge in "Structure and function in the nervous systems of invertebrates". Six pictures were used by Bloch and Cuskey, who wrote the chapter "Cardiovascular system" in the two-volume work "Creps Textbook of Histology", published in New York.

A valuable and much-admired part of ÁBRAHÁM's research work consists of the internationally unique collection of more than 19,000 neurohistological preparations, part of which is known everywhere throughout the world. In this a large proportion of the organs of almost every typical representative of the animal kingdom are treated. Some of the preparations are unique, and the majority of them display the greatest degree of perfection attainable with neurohistological techniques. Much of the material is Hungarian in origin, but there are some specimens which he obtained for processing from Los Angeles, Cleveland and London. Among the preparations are some prepared in Naples when ÁBRAHÁM carried out neurohistological examinations at the Hungarian bench in the Stazione Zoologica in 1938.

The preparations are arranged in four cupboards in Professor ÁBRAHÁM's laboratory. Cupboards, preparation holders and preparations are all numbered. The first cupboard contains preparations prepared from human organs. Among these practically every organ of man is represented. In the same cupboard follow the domestic mammals, and the more-easily accessible forms living in the wild. In the second cupboard are the other mammals and the birds. In the third cupboard are arranged the birds, the reptiles, the amphibia, the fish, the molluscs, the echiodermata and in part the arthropoda. The fourth contains the other arthropoda and the worms. Also arranged in this cupboard, under the label "appendix", are those preparations not fitting into this classification. Next follows the "Spetialia", the preparations shown abroad and those from which drawings and photographs were prepared for his lectures and publications. The entire collection consists of neural preparations; only in the fourth cupboard are there a few hundred section which deal with the neurosecretory systems of the insects, in addition to their nervous systems. At the end of the collection are the more than 350 stained preparations, which were the very first histological preparations of ÁBRAHÁM. These were prepared in part for his doctoral dissertation, and in part for demonstrations. A large proportion of the preparations were prepared by ÁBRAHÁM himself, but particularly in more recent years he has received much help from his coworkers. As a result of his activity an ÁBRAHÁM school of comparative neurohistology has developed. The collection is extremely valuable. The preparations deserve every protection, for they are irreplaceable, they contain much that is new, even after what has already been published on them, and they serve as the basis for electron-microscope examinations. But there is also another reason why this valuable treasure must be preserved and highly estimated, and in this unforgivable sins have been committed. Even before ÁBRAHÁM there were neurohistologists in Hungary. One was TIVADAR MARGÓ, who dealt with the innervation of insect muscles. Not one of Margó's preparations has survived. Another was MIHÁLY LENHOSSÉK, who was one of the founders of the neuron doctrine. It is not possible to see even one of Lenhossék's preparations. Ábrahám's departmental predecessor was the famous neurohistologist ISTVÁN APÁTHY. His preparations too have been lost in the main. Altogether only a few have remained, and even these were acquired with some effort by ÁBRAHÁM; they are now kept in the drawer of his writting-table. It was due to great thoughtlessness and negligence that these preparations, which were of such high value, have disappeared. It would be a serious and unforgivable crime against Hungarian science and culture if a similar fate awaited the neurohistological preparations produced by ÁBRAHÁM and his school.

Professor Ábrahám's grandeur, and his ability and efforts to develop an ideology on the basis of what he saw and experienced, were expressed in his love to watch

what others were doing elsewhere, and also how they did it. He loved objective comparisons for, as he often put it, these are the bases and measuring units whether what is done at home is of value, is of permanence, and makes a contribution to men being better and the earth more beautiful. On a number of occasions he visited Germany, Bulgaria and England, and he also went on trips to Italy, Austria, Rumania, India, Czechoslovakia, France, Belgium, Holland, the Soviet Union and the United States. In 1930 he delivered a lecture at the Eleventh International Zoology Congress in Padua. He was member of the international zoology congresses in Lisbon, Paris and Washington. In 1956 he spent a month in Rumania, during which he gave lectures at the Academy of Sciences and the Medical University, and held demonstrations on neurohistology in the Department of Histology in the Medical University, in the Pavlov Institute, in the Physiological Institutes of the Academy and the Medical University, and in the Department of Endocrinology, and in the Department of Comparative Anatomy and Histology in the Biology Faculty in Bucharest. He held neurohistological demonstrations in the Departments of Histology and Forensic Medicine of the Medical University in Jassi, in the Department of Anatomy of the Medical University in Marosvásárhely, in the Physiological Institute of the Bólyai University in Kolozsvár and in the Department of Histology of the Medical University in Temesvár. In 1957 he participated in the congress held in London to commemorate the 300th anniversary of the death of Harvey. At the same time he gave neurohistological demonstrations in the University Anatomy Department in Oxford, in the Medical Research Institute, and in the Department of Biology of the Medical University in London. In 1958, at the invitation of the Ministry of Health, he spent two weeks in the People's Republic of Rumania. During this time he delivered lectures to the Morphological Society at the Medical University in Jassi, and at the First Rumanian Congress on Psychiatry and Endocrinology. On the same visit he held discussions and demonstrations in the Department of Histology in the Medical University in Jassi, and in the Department of Comparative Anatomy and Histology at the Biological University in Bucharest. From 20 January until 12 February 1959 he paid a visit to India. In Delhi he participated in the 46th Indian Science Congress, in Bangalore in the Golden Jubilee of the Indian Science Institute, and in Agra in the Festival Meetings of the Indian National Academy. During his stay in India he held lectures and neurohistological demonstrations in Delhi, Bangalore, Agra and Bombay. In 1960 he gave a lecture in Brno at a symposium dealing with the methods of theriological research, and organized neurohistological demonstrations in the Department of Anatomy at the University. In 1961 he delivered a lecture at the Eleventh International Congress on Entomology in Vienna. From 13 to 28 February 1963 he visited England as a guest of the Royal Society. He held lectures and neurohistological demonstrations in Aberdeen, Edinburgh, Cambridge and London. In July 1963 he delivered a lecture at the international conference "Modern Trends in Neuromorphology", arranged in Budapest on the occasion of the 100th anniversary of the birth of Mihály Lenhossék. In September of the same year he lectured in Brussels at the "Seconde Réunion Européenne d'Endocrinologie Comparée", and in Sofia at the "V. Symposium International des Histologists". In August 1964 he took part and gave a lecture in the "II. International Kongress für Histo- und Cytochemie in Frankfurt am Main." In July of the same year he participated and lectured at the XII. International Congress of Entomology in London. In May 1965 he delivered a lecture at the First Romanian Congress on Animal Physiology. In July 1965 he lectured at the 2nd Conference of Anatomists and Histologists in Sofia.

In the following month he took part in the International Symposium on Phylogenesis and Ontogenesis of the Forebrain in Frankfnrt am Main – Niederrad. By invitation he gave a lecture on "Phylogenesis of the nerve cell". In November 1965 he participated and lectured in an international symposium on Baroreceptors and hypertension in Dayton, USA... After the symposium he gave lectures in the university in Columbus and in Clevland at the Annual Meeting of the High Blood Pressure Society. He held lectures in the University and the Department of Physiology in Philadelphia. In July 1966 he lectured at an international symposium on Arterial chemoreceptors in Oxford. In 1967 he participated in the Third Conference of Anatomists and Histologists in Plovdiv, Bulgaria. In August of the same year he gave a lecture at the Fourth Conference of European Comparative Endocrinologists in Karlsbad. During July 1968 he spent 10 days in Leningrad and in the course of this visited the Pavlov Morphological Institute in Koltuschi. He lectured to the staff of the Institute, discussed their research work, inspected their preparations, and provided information and advice. In March 1969 he gave a lecture at the 54. Congress of the Association of Anatomists in Sofia, and in August of the same year participated and gave lecture in the Fifth Conference of European Comparative Endocrinologists in Utrecht. In August 1970 he lectured and was section chairman at the Ninth International Congress of Anatomists in Leningrad. In 1971 he was section chairman and delivered a lecture at the Sixth Conference of European Comparetive Endocrinologists in Montpellier, and in August 1971 he took part in the Seventh Conference of European Comparative Endocrinologists in Budapest.

Professor ÁBRAHÁM continues his work. His research areas remain the nervous system, the cerebral cortex, the synapses, the receptors, neurosecretion, the cardiovascular system and the sense organs.

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István Apáthy
TRIBUTE TO HIS MEMORY ON THE OCCASION OF THE 50TH ANNIVERSARY OF HIS DEATH*

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September 27 marked the 50th anniversary of the death of István Apáthy, the founder of the Department of Zoology at Szeged University, an excellent zoologist, an outstanding neurologist, and in his time the greatest microtechnician in the world. As the second successor in the Department, and as a researcher working in the same field, it falls to me to pay tribute to his memory on the occasion of the 50th anniversary of his death.

I. Apáthy is one of the eminent figures of Hungarian scientific life, well-known internationally, and regarded with honour and esteem. His life was full of struggles, sufferings and afflictions, but it was also rich in esteemed creations and values; the rapid passage of time has done little to detract from these, and indeed, if the facts and the honest strivings are considered, it must be stated that they have increased and become enhanced. He was a professor, and one of the best, who attained this high position at a relatively early age. He was a true research worker, who throughout his life was enthralled by the noble problems of the science of life. He was a pragmatic scholar, who everywhere and in everything sought the interdependences, the overall relations and the connections.

He was born in Budapest on January 4, 1863. After completing his secondary-school studies, he enrolled at the Medical Faculty of Budapest University. During his university years he studied with diligence and ambition, and as he was born a dominant personality, with his outstanding abilities he soon became one of the widely respected leading figures among the university students, who proclaimed and urged the need for the independence of Hungary in the political movements. After completing his basic studies, he entered the Department of Pathological Anatomy at the University, where he carried out animal histological examinations under the effect of initiatives received from Professor Margó. He had still not obtained his medical diploma when, in 1884 at the age of 22 years, he published a paper of more than 100 pages, under the title „Tanulmányok a Najádeák szövettanáról" ("Investigations of the histology of the Najades"), in the collected series produced by the Hungarian Academy of Sciences „Értekezések a természettudományok köréből" ("Treatises on the natural sciences"). At about this time he also published „Az út a révpart felé. Klinikai képek" ("The way to the roadstead. Clinical pictures"), a shorter literary work, in which, on the basis of what he saw and heard in the wards, he deals with the then social conditions and with the problems of the locally occurring poverty and social destitution. This work was closely followed by poems of various lengths, which later increased both in number and in

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value, for I. APÁTHY was a poetic soul, who throughout his entire life was inspired by the Muses, even when he was carrying out researches in the laboratory and when he was fighting difficult and passionate battles in the political life. In 1885 he acquired his medical diploma, and followed his inclination and enthusiasm for zoology by becoming assistant to the then professor of zoology and comparative anatomy, TIVADAR MARGÓ.

At that time T. MARGÓ dealt with the peripheral nervous systems of the insects and it is probable, therefore, that I. APÁTHY here received those impulses which later directed him towards his researches into the nervous systems of the invertebrates. After only one year as an assistant, in 1886 he joined the Stazione Zoologica in Naples, where with only a few breaks he worked for three years. The director of the institute, ANTAL DOHRN, wished a monograph to be prepared on the fauna and flora of the Bay of Naples, and since Apáthy's earlier work was directed towards such a field he was entrusted with the treatment of the taxonomy and anatomy of the leeches. APÁTHY liked this theme and thus began a systematic treatment with great pleasure and enthusiasm; of tremendous help to him in this, of course, were his rich knowledge in this respect, which he had gained in Budapest, and his already notable microtechnical ability and skill, which characterized his comprehensive genius and led and guided his particularly dexterous and practised hands. As a result of his love for the subject, his talent, his skill, coupled with great diligence, and his considerable familiarity with the literature, in the first three years he spent in Naples I. APÁTHY wrote some 17 scientific papers. Among these was his pioneering publication „Nach welcher Richtung hin soll die Nervenlehre reformiert werden", published in „Biologisches Centralblatt", which had a revolutionary effect on neurohistology. This was followed by „Das leitende Element des Nervensystems und seine topographische Beziehungen", similarly prepared in Naples, and published in „Mitteilungen aus der Zoologischen Station Neapel", Volume XII.

During the time spent in Naples he visited the Swiss, German, Belgian and Dutch universities and the scientific institutes in Paris. The period in Naples was suitable not only for him to carry out high-level investigations in the zoological sciences, but also to acquire a store of knowledge through his experience whereby he could reassuredly undertake the leadership of a university department at a later opportunity. Such an opportunity was not long delayed. In 1890 the Chair of the Department of Zoology in the University of Kolozsvár fell vacant, and I. APÁTHY was appointed to fill this vacancy at the age of 27 years. This appointment was followed some years later by another, when the leadership of the Department of Histology and Embryology too was entrusted to him.

The place he had come to was a little confined. It was particularly confined for that I. APÁTHY who was already acquainted with practically all of the universities in Europe, and who was already recognized, by virtue of his work and through personal meetings, by every respectable research worker in Europe. The Department of Zoology in the University of Kolozsvár was at that time housed in the Count Mikó villa. The department was very restricted for space, and the equipment was scandalously insufficient. Apáthy's aptitude, talent and foreign experience, however, provided a guarantee that the small Mikó College would rapidly expand, and that the results arising from the diligent work there would soon go out into the world. And this quickly came to pass. With all the requisite steps being taken, and if necessary with struggles and battling, the small department was soon equipped with everything desired, and the possibility even emerged of foreign guests being able to carry out

research work there. Places constructed for three such guests, and these were provided with all the necessary equipment for the microtechnical and histological investigations begun and directed under his leadership. The reputation APÁTHY had acquired in Naples, together with the personal contacts, led to many foreigners seeking out this small department, either to learn from what they saw there, or to master the APÁTHY microtechnical procedures. Among the first to appear in the department was the German, Bethe, one of Apáthy's greatest admirers, who remained a faithful devotee and disciple until the end of his life. Among others to visit the department were BOEKE, the later famous DUTCH neurohistologist from Amsterdam, PLATON STEWARD from Baltimore, MOLLIER and HASSELWANDER from Münich, JORIS from Brussels, KOVALEVSKY from Russia, GODLEVSKI from Cracow, SEMEN JEFIN LONDON, the Russian research worker, and ANNA KROSSUSKAJA, assistant to PÁL LESSHAFT, the Director of the Anatomical Institute in Leningrad. Another Russian, KOROTNEFF, sent his leeches collected from Lake Bajkal to APÁTHY for processing. Others to make pilgrimages to Kolozsvár included RIMOTTI and WALDEYER, Professors in Anatomy at Pisa and Berlin, respectively, and V. VIDAKOVICH from Buenos Aires. The visitors and research workers going to the department were attracted not only by the special research equipment, most of it made in Kolozsvár, but also by the special research methods, known as the APÁTHY procedures, which at that time were to be found en masse in the various journals and methodology books. They were also attracted by the person of Apáthy himself, who, with his gracious manner, his great knowledge and his extraordinary microtechnical skill, together with his personal endowments, which were particularly suitable for systematization and shedding light on the routes and directions to overall truths, captivated all those who came under the spell of his sparkling wit.

Although now perfectly equipped, the small Mikó college was in no way sufficient to provide a home for Apáthy's intentions, abilities, knowledge and comprehensive plans. Using his strongly enhanced respect before even the state leadership, he therefore did everything to ensure the financial basis for the creation of a Department of Zoology which he considered fit and appropriate for his research and teaching work. His unflagging efforts led to success: in 1909 a new Department of Zoology was established in Kolozsvár, the like of which was rarely to be seen throughout Europe at that time. In its exterior too this department differed from the others. The enormous two-storey building was provided with loggias and experimental earth-baths. There were balconies on every floor, and from spring to autumn the roof, walls and balconies were covered with flowers. In one part of the building a constant-temperature, deep cellar was fitted out, and the large basement was furnished for the experimental animals. In addition, there were special installations for the fresh-water and sea-water aquaria. The ground-floor of the building housed the wonderful zoological collection of the Erdélyi Museum Society and the lecture rooms. On the first floor were the students' work-rooms, the library and the administration offices. The second floor held four laboratories for those who carried out scientific investigations into their own themes. The living-quarters of the Director and his assistants were also to be found on this floor. The outfitting of the department was totally individual, and was prepared in accordance with original conceptions and plans. Everyone who saw it received the impression that as regards its form, its structure and its installations this department was quite original, and differed from all other departments of a similar nature in Europe. I. APÁTHY took pains not only with the beautiful new department, but also with provisions for his im-

pecunious students to be able to study free from financial worries. Thus, he created a cheap cafeteria for them and later, with the assistance of some friends of similar disposition, a modern students' hostel.

Under Apáthy's leadership serious teaching, pedagogic and scientific work continued in the new department for a long period. However, this work was later disturbed somewhat, both by the political actions of APÁTHY, resulting from his character, and also by the events which followed the First World War. Under the terms of the Peace Treaty of Trianon, Transylvania, Kolozsvár and hence the Kolozsvár University became Rumanian, while I. APÁTHY fell into Rumanian captivity for some months during the events associated with the annexation.

If we wish to assess the value of Apáthy's work during his career, then it is necessary to consider three fields where he was truly great, and where he produced lasting scientific results of immense worth. These three fields are those of zoology, neurohistology and microtechniques.

I. APÁTHY began his zoological investigations in Budapest and continued them in the Stazione Zoologica in Naples. These studies referred to the taxonomy and anatomy of the leeches. Apáthy collected the necessary material from the Bay of Naples and from Hungarian waters. Part of this material was preserved in the customary way, but the vast majority of it was fixed, embedded and subjected to histological processing. His papers which appeared on this topic were received with great interest and appreciation by his fellow-specialists. Kovalevsky, the noted Russian zoologist, described Apáthy's investigations as classical (Étude Biologique de l'Haementeria. Mém. d. l'Acad. imp. d. Scienc. d. St. Petersb. VIII-e ser. vol. II. N. 1. p. 40). Leuckart and Perrier too rated this work of APÁTHY highly, and used his results in their own papers.

His studies on the intestinal tract of the sea leech, *Pontobdella muricata*, with the aid of his gilding procedure, were of a pioneering nature and produced an almost evolutionary effect in the international literature. He was the first to stain with wonderful definition the intestinal nervous system of this leech. His preparations, the most beautiful of which are in my possession, even now still reveal the extreme definition and clarity of the intestinal nervous system and of the connection of this with the tissues of the intestinal wall. In my view this fact alone would be enough to make the name of I. APÁTHY of lasting fame, to ensure the positive international appreciation of his work, and to confer on him objective esteem. However, this is not all that I. APÁTHY discovered in connection with these investigations and established in durable form. He succeeded in proving and having accepted in his own age that fine fibrils (neurofibrilla) run parallel, or arranged in a network, in the protoplasm in the nerve cells, in the sensory cells and in their processes. Others before APÁTHY had considered the possibility of such formations. From the striation in the processes of the nerve cells, MIKSA SCHULTZE had regarded that there might be fine fibrils (primitive fibrilla) here, but in the absence of a suitable technique he was unable to demonstrate these. After osmic acid fixation Kupffer stained the primitive fibrilla in the myelinated fibres of the vertebrates by acid fuchsin but that such existed and could be detected in the nerve cells was due exclusively to I. APÁTHY.

APÁTHY considered the neurofibrils to be the conducting elements of the nervous system. Indeed, he went further in the morphological and physiological evaluation of the neurofibrils, and announced that these cross the cells, the centres and even the myofibrils and thereby form a connected system, which traverses the entire

organism and interlaces the total nervous system, together with all its elements, into a continuous unit. Apáthy's discoveries declared war on neurondoctrine and the study of synaptology, i.e. the transfer of stimuli by means of contiguity, and initiated tremendous battles of extreme intensity, which lasted over a long period, mainly between himself and such outstanding representatives of neurondoctrine as RAMÓN Y CAJAL, MIHÁLY LENHOSSÉK and others. In this brief appreciation, there is little room for us to give a detailed treatment of who was right in this question, mainly because we too are neuronists. However, it must be said that in our opinion of this affair APÁTHY, in revolutionary mood, overstepped the limits and possibilities objectively permitted by his preparations, which referred exclusively to leech material. We consider, and this is confirmed by the APÁTHY preparations in our possession, prepared from the intestinal tract of *Pontobdella muricata* in Naples in 1882, that APÁTHY overlooked certain facts and features when he reported cells in the intestinal wall which the fibrils (neurofibrilla) traverse continuously, continuing without interruption into the organism. APÁTHY gilded the intestines totally, in the form of a membrane, and thus worked on thick material; in this way there resulted drawings such as those published in his work „Das leitende Element des Nervensystems und seine topografische Beziehungen zu den Zellen". The great fight, which began with the appearance of the above work, was decided essentially in favour of neurondoctrine. The nerve pictures obtained with more recent procedures, the changes resulting from experimental intervention, and in particular the pictures obtained with the electron-microscope, indicate that there is no continuity, and that neurondoctrine has complete validity in both anatomical and physiological respects. As one who has spent more than 40 years in investigating almost all classes and organs of the animal kingdom, I have constantly held the view since the commencement of my research work into the histological structure of the nervous system, that there is neither plasmatic, nor dendritic, nor neurofibrillar continuity in the nervous system. All nerve pictures reporting such a continuity are either based on an oversight, or are the results of an inadequate technique. As regards the neurofibrils, I considered that these exist, but that they are not always apparent and never leave the region of the nerve cells. They are simply constituents of the neuron, just like the tigroid, the cytocentre, the Golgi reticulum, and the others. In spite of this, as a worker in a similar field, and as I. Apáthy's second successor in the Department, I acknowledge and proclaim that as a neurohistologist he performed pioneering work. It was he, who with his own gilding method first demonstrated to the world in an outstanding manner and with practically unsurpassable clarity and definition the intestinal nervous systems of the worms and the neurofibrils in the motor ganglion cells of the medical leech *(Hirudo medicinalis)*, and who, with his studies based on these investigations, initiated such a revolutionary movement in the field of comparative neurohistology, leading to intense battles and hence to the elucidation of the fundamental concepts. His nerve-investigation methods, pre- and post-gilding, can still be used today, but as he himself frequently emphasized, success demands a particular situation, much work, infinite patience and a special love of the subject.

The third field in which I. APÁTHY excelled was that of microtechniques. The preparation of organs and tissues for microscopic examination caused many headaches to those who attempted with good-quality magnifying systems to make the material the subject of a more thorough study. It required considerable ingenuity to devise those procedures which, at least in the main, inhibited the extensive contraction of cell-groups passing from life into death, and provided the means and possibility

of preparing thin, transparent sections from the material, so that the entire sections might be arranged in consecutive order and systematically studied. Nor was it a lesser problem to purify the prepared sections from the material necessary for the preparation, or to stain them in such a way that the individual constituents of the cells, large and small alike, should come under the magnifying lens of the microscope sharply distinguished from one another, and in a well-differentiated form. Another major problem was how to produce the impregnated or stained sections in a durable state, suitable for preserving for examination over a long period. Particularly in the beginning, the fixing, the embedding, the sectioning and the preserving all caused much thought to those who wished to see and study the structures of the tissues and the cells in a state and form at least somewhat approximating to those in the living condition. Much experience, many efforts and much ingenious conception was necessary for the histological and cytological examinations to acquire a firm basis, and for the findings to be accepted as fact and used as a sound foundation in the physiological and genetic studies. Many had worked in this field prior to I. APÁTHY, and many utilizable methods and procedures had come into the hands of the research workers, but it must be stated objectively that there had been extremely few histologists and cytologists who surpassed I. APÁTHY in care, accuracy, inventiveness, ingenuity and skill. He attended to the compositions of the fixants, to the development of these for the different animals and different organs, to the selection of methods for the complete removal of the fixant materials, to the preparation of the paraffin for embedding, to the establishment of the desired temperature, to the position of the microtome knife, to the arrangement of its honing plane, to the honing, to the staining, to the washing and to the preservation with accuracy and precision, so that everything he did in this field was a standard example of how one must work with microtechniques in order to produce results. As a consequence of the careful embedding, the correct preparation of the microtome, and the correct honing and accurate adjustment of the knife, they were able (as one of his students writes) to prepare 4000 sections in the Apáthy department at Kolozsvár from skin one millimetre thick, or from a "nerve fibre", while sections of the thickness prepared at that time in foreign laboratories could readily be split into four sections. The experience and results emerging from Apáthy's work, which have become exemplary for those wishing to learn, are generally recognized and many of them are still of great use. I am thinking here of double embedding, triple staining, gilding, etc. All this shows extremely clearly that I. APÁTHY was a brillant thinker, a reasoning and theorizing research worker, and a man who did things on a grand scale, who in all cases himself tried to plan and to create the instruments, the apparatus and the procedures whereby he could obtain an answer to the given questions of living nature. However, he then became really great as a microtechician, and known and recognized the world over, when he chronicled the empirical results and experimental facts acquired by himself and others, reviewed them and subjected them to criticism, and thereby raised the microtechnique to the rank of a science. His activity in this respect gave rise to his two-volume work on microtechniques „Die Mikrotechnik der tierischen Morphologie" (Abt. I. 1896; Abt. II. 1901).

As to the value of this publication, it is quite unnecessary even today to explain this to anyone working in this field. It is a systematic, exact and clearly written, outstanding work, which from the viewpoint of the present has only one main fault; as a result of the unfortunate turn of events the planned third volume was not produced. It is easy to conceive the significance of this work in its own time; it

was truly a bible, in which all of use and value in a microtechnical line was diligently treated. It was a guide, an example and a tutor to all those who found pleasure and strength in the cultivation of this wonderful auxiliary science, and in general in the dissection of the great biological problems. With regard to the actual opinions of the then specialists concerning this work, we can do no better than to let them speak for themselves. Schaffer introduced his review of the book (Wiener Klin. Wochenschr. Jahrg. XV. N. 12. 1902) with the following sentences: "The microtechnique is on its way to becoming a science. This is a characteristic text-book which, by treating the subject historically, critically and theoretically, raises it to scientific level." Heidenhain, the Tübingen histologist, wrote as follows (Münchener Medic. Wochenschr. Jahrg. 44. 1897): „Das Buch ist eine vorzügliche Arbeit, eines besonnenen und erfahrenen Gelehrten ist ausserdem nicht etwa trocken geschrieben und wir haben soviele vorzügliche Bemerkungen allgemeinen Inhaltes darinnen gefunden, dass unserer Meinung nach, auch der vollkommen durchgebildete Techniker das Werk mit Vergnügen lesen wird." On page 257 of the volume of the "Royal Microscope Society" for 1902, the following can be read as to the microtechnique of I. APÁTHY: "The facts, which are arranged in chronological sequence, are positively astonishing in number and their mere enumeration tells of the extraordinary labour which the author has bestowed on the work on the knowledge of the subject exhibited therein." PAUL MAYER, the grand-master of the microtechniques, in 1920 named APÁTHY as the greatest living microtechnician. M. LENHOSSÉK, the excellent neurohistologist, who as a neuronist was diametrically opposed to APÁTHY and fought tooth and nail with him, in his appreciative commemoration of him refers to I. APÁTHY as a microtechnician "magister mundi".

With what has been said so far we have in effect finished with I. APÁTHY as a great organizer, a research worker and a scholar. If anything remains to be said, it is only that thanks must be offered to Fate for blessing Hungary with such a great spirit, and such a comprehensive and internationally appreciated individual. If nevertheless we sense a little sadness at the thought of the name of I. APÁTHY, this arises from two sources: the first is that during the First World War and in the final decade of his life he dealt more with politics than the world of microscopes and the laboratory could allow without a little neglect; the second is that his death came far too soon. He was released from his imprisonment in Szeben in 1920 and came to the University of Szeged where, with the books and equipment which he brought with him, he strived to organize his third department of zoology in a building temporarily assigned for that purpose. However, this no longer proved possible. I. APÁTHY was a sick man, both physically and spiritually. He had long suffered from heart trouble, while psychologically the changes and sufferings preyed on his mind and tormented him. The sufferings were increased by the unjust procedure whereby his favourite subject, the histological lectures, was taken away from him and given to others, who were not his supporters. Even under such conditions he attempted to serve his popular science and poetry, with both heart and soul. In the twilight of his life he wrote one of his most beautiful poems „Az elszalasztott kikelet" ("The missed spring-time"), in which, meditating on the problems of existence, he raises the cruelly tormenting question: if he becomes old and incapable of "work and battle", will there remain for him "another spring", and will there be time for him to be able to enjoy the awakening, "May and the roses"?

His own poignant words grimly foretell the negative answer to the question: „ott halok meg egy bús november alkonyán s lelkemben elfagy élvezetlen a tavasz,

melyet úgy kíván" ("for I shall die one sad November evening, and the spring it so desires freeze in my spirit").

In the final years of his life he sought the balm for his gaping wounds between Szeged and Naples, but he could no longer overcome the ever increasing infirmities and anguished sufferings. He died on September 27, 1922 after long suffering. With his death an ardent intellect and a far-shining beacon left the stage of Hungarian science, but his spirit lives on among us and everywhere throughout the world where science is loved, and for this man is fired, will work and if necessary fight.

The cells comprising the nervous system, over the differentiation of which so many battles ensued, have by this time been reduced to a common denominator. The „nerve cells" have become Schwann cells, which serve to the capsule of the vegetative axons, linked to them by the mesaxon ducts, while the „ganglion cells" have been called nerve cells respectively neorons.

Neurondoctrine, against which so many bitter struggles were fought, has proved correct. The vesicles grouped in the synapses and the membrane thickenings on the axon terminals or on the cells and the dendrites have provided the final and irrefutable series of evidence in favour of contiguity.

The existence of neurofibrils can be proved only by impregnation, but even then not generally and only under the light-microscope. Under the electron-microscope the proeesses of neurons appear empty, while the fibrosity is represented in the neurites by the neurofilaments and in the dendrites by the neurotubules. The neurofibrils can not be seen in the body of the nerve cells; their place is probably occupied by the ducts of the endoplasmic reticulum and the tube systems belonging to the Golgi complex, or these may have been the formations considered as neurofibrils under the light-microscope.

The fixing and embedding, with their associated many types of skilful, delicate and complex activity, are slowly but progressively becoming outdated. In their place have come the freezing-microscope and the refrigerator, with which it is possible to prepare sections of convenient and necessary thinness for even the finest examinations. The stainings and impregnations too are slowly losing ground. Their place is being taken by the electron-microscope and histochemistry. Of the many endeavours and the great variety of procedures and modifications, only the Golgi method has withstood time, for this gives the most utilizable basis for the electron-microscope examinations.

The work carried out by I. APÁTHY in his researches into the structure and operation of the nervous system, and the struggles which he waged for this, were not unfruitful and for nothing, for he directed the attention of anatomists, histologists and physiologists throughout the world to the nervous system. It is a consequence of the ardent work of APÁTHY and others that research into the nervous system has today become a central theme internationally. Throughout the world at present great energy and particular diligence are devoted to investigations into the structure and functions of the nervous system, that wonderful and tremendous sphinx, who is so reluctant to give up her secrets. Whether or not this will lead to a result, and if so what and when, we cannot say. One thing, however, is certain. Regardless of whether an answer be attained, the work which I. APÁTHY carried out in his researches into the nervous system and in the field of the knowledge and reporting of the histological structure of the animal organism remains lasting, valuable and undying.

On the occasion of the 50th anniversary of his death, in the name of every anatomist, neurologist and histologist of Hungary and the world, with gratitude and respect I bow my head in recognition of his memory.

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COMPARATIVE WEED INVESTIGATIONS IN WHEAT AND MAIZE CROPS CULTIVATED TRADITIONALLY AND TREATED WITH WEEDICIDES
II. CHANGES IN THE WEED VEGETATION OF MAIZE CROPS

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Abstract

Coenological studies were carried out on several state farms to establish the changes in the weed-vegetation on the socialist reorganization of agriculture, with regard to the more modern large-scale agrotechnology, and also to chemical weedicides (Simazin, Atrazin). The results were compared previous data for the same sites, and the following conclusions were drawn.

During 15 years the weed-cover of the maize crops decreased significantly as a result of the more modern large-scale agrotechnology. The decrease took place in the perennials wintering in the soil (G).

In crops first sprayed with Hungazin PK (Atrazin) a further decrease of almost 50% (compared to the traditionally cultivated crops) occured in the weed-cover; this was due to the annuals (T), the perennials remaining unchanged.

Simazin and Atrazin treatment for several years resulted in very unfavourable changes in maize monocultures. Although the total weed-cover showed little change compared to the traditionally cultivated data, its composition shifted in a negative direction, for the cover of the perennials wintering in the soil (G) increased to about two and a half times that of the control.

Investigations in 1961 showed that a very considerable decrease resulted in the weed vegetations of wheat and maize crops on the effect of large-scale agrotechnology in addition to traditional cultivation, compared to the national weed survey of 1947—1953 (FEKETE, 1963). As already reported in the publication dealing with the first part of the investigations (FEKETE, 1973), the main aim of these researches was to establish the extent of the role of a more developed large-scale agrotechnology in the change of the weed vegetation, and that of the application of various chemical weedicides (2,4-D and aminotriazines), since besides the agrotechnology the state of the weed vegetation is affected considerably by the ever increasing use of the different herbicides. Further justification for these researches was the fact that in connection with Simazin and Atrazin, and the identical Hungazin DT and Hungazin PK, a number of important problems required elucidation.

At the time of the commencement of the investigations (in 1963) it was generally held that with triazine chemicals (independently of the composition of the weed flora) it was possible to rid maize crops completely of weeds (UBRIZSY, 1960; 1962; UBRIZSY et al., 1961; VIRÁG et al., 1960; 1962; SZIGETHY, 1961; 1963). Data were not available with regard to how the weed vegetation of an area changes if aminotriazines (Simazin and Atrazin) are applied on it for a prolonged period, although just this method of treatment had been proposed for maize (VIRÁG et al,. 1962), and in practice certain farms had turned over to this method. Since this problem had not been clarified up to the beginning of the investigations, besides the traditional and the first-year chemically treated maizes, increased attention was devoted to the study of the weed relations of such crops under large-scale farming conditions.

Materials and Methods

Weed coenological surveys were carried out with the BALÁZS (1944) scale from 1963 in traditional maize crops and in others freed from weeds at various times since with Simazin and Atrazin (Hungazin PK). The sites and methods of investigation were reported in detail in the earlier publication dealing with the results for wheat crops (FEKETE, 1973). It is necessary to add only that apart from the state farms mentioned surveys were carried out everywhere in plots on cooperative farms employing traditional cultivation. Since only sparse data are available on the weed conditions of maize crops at the beginning of summer, in contrast with the national weed surveys investigations were performed twice during the growing period, at the beginning of June (survey 1) and in the second half of August (survey 2). Those weed species were listed from the results obtained, which occupied an area greater than 1% in an average compiled according to treatment for the investigated sites (Table 1), and in addition the distribution of the weed cover according to life forms is also reported (Table 2) in the classification of ÚJVÁROSI (1952).

The soil and precipitation conditions were also reported in the earlier publication. In connection with the precipitation, however, it must be pointed out that at the time of the national weed surveys (in 1950) the weather was predominantly extremely arid and in part of the investigated sites (Fehérgyarmat, Mezőnagymihály, Lábod and Kaposvár) in general 200—300 mm less precipitation fell up to the end of the growing period than in 1963. The total precipitations in 1963 corresponded to the 40-year averages for these areas, being somewhat more than the average at Mezőhék. Even in this year, however, conditions were not favourable everywhere for the effects of the Hungazin chemicals to be exerted, for at Lábod in April, for example, only 12 mm of rain fell (13 mm at Kaposvár), and May too was dry.

In connection with the agrotechnological data, it should be mentioned that in the maize crop areas (with the exception of those sprayed at Enying from 1962) the autumn deep ploughing, the spring soil cultivation preceding the sowing, and the sowing itself were performed in good time and with the required quality. In the former-mentioned area, however, the maize treatment involved spring ploughing. The traditionally cultivated maizes, again with the exception of Enying, were subjected to two or three mechanical, and two manual row-hoeings. At Mezőnagymihály and Kaposvár hoeing was carried out over the whole area of the traditional maizes a few days before the first surveys. At that time the crops at Fehérgyarmat, Mezőhék and Enying had been subjected to cultivator treatment only once, about 2—3 weeks before, while those at Lábod had not yet been hoed. In these latter four farms the first hoeing was performed immediately after the first surveys, and the second at the beginning of June. In contrast with the normal practice, at Enying the chemically treated maizes too were hoed the same number of times as the traditional ones there: two mechanical and one manual hoeing was applied, with the difference that up to the time of the first surveys the chemically treated maizes received one hoeing over the whole area, while the traditional ones underwent only one cultivator treatment. It is very important to take this into consideration, therefore, in the evaluation of the June data for the chemically treated maizes.

The amounts of chemicals applied are given in the text.

Results and discussion

1. Effect of large-scale agrotechnology on the development of the weed vegetation in maize crops

a) Weed conditions of traditionally cultivated maize crops at the beginning of summer

The distribution of the weeds found at the beginning of June according to life forms is shown by survey 1 of Table 2 and by Fig. 1. It is clear from these that even then the late-summer annuals (T_4) are present in greatest numbers (10.8%), since they comprise almost half of the total cover. The relatively low value (5%) of the cover for the spring-sprouting early-summer varieties (T_3) compared to the late-summer forms is in effect due to the fact that at the time of the first surveys only at Lábod was the soil of the maize crops untouched. As a result, only here did the spring-sprouting early-summer varieties occur in bulk (22.79%). In contrast, where

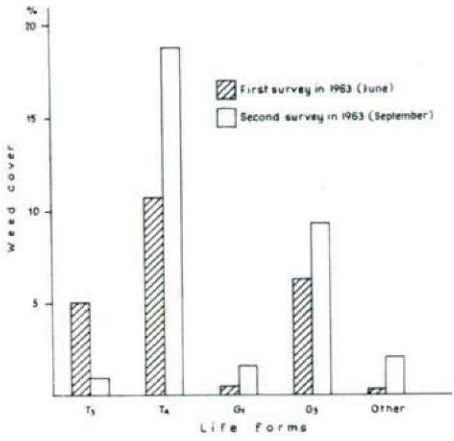

Fig. 1. Comparison according to life forms of the early- and late-summer weed conditions in traditionally cultivated maize crops.

the crops had already received one interrow hoeing, the species belonging to the T_3 group occurred in lesser amounts, and mainly only in the rows. This shows that from the sowing of the maize until the first hoeing the T_3 life-form occupied a much larger area in the investigated sites. The above weed cover at Lábod consisted also entirely of *Raphanus raphanistrum* (21.87%), and at the other sites of *Sinapsis arvensis*, as typical members of the early-summer (second) aspect.

In June the perennials played a much smaller part compared to the annuals in the development of the weed cover, and among them only the root-like couch-grasses (G_3) were significant (6.25%).

b) Late-summer weed conditions of traditionally cultivated maize crops

According to the surveys in 1950, at the end of the growing time in the maize crops of the investigated sites 78 weed species lived, with a cover of 42%. According to the combined data, there were now 97 weed species, with an average weed cover of 32.6%. As can be seen from the data, during the intervening nearly one and a half decades the weed cover of the maize crops decreased by 24% as a result of the more up-to-date large-scale agrotechnology (Table 2, survey 2). The decrease in maize crops, therefore, was not so extensive as that in wheat crops, or as that experienced in both cultures in 1961 (FEKETE, 1963; 1964 manuscript; 1973). On the other hand, the number of species was now increased.

Comparison of the results with the data of ÚJVÁROSI for 1950 led to the following findings:

The cover of the spring sprouting early-summer varieties (T_3) increased by a factor of two compared to the value for 1950, while that of the late-summer ones (T_4) (in contrast with the investigations in 1961, when a very considerable decrease was found for all weed groups) remained essentially unchanged (18.58% and 18.76%). The fact that the annuals did not decrease involves two factors. One of these, as already indicated, is that 1963 was much wetter than 1950. The other was that because of the limited nature of the crop-rotation, maize had been grown continually

by the traditional way in some (3) farms in these areas since 1961. In this respect it is known that this favours just the accumulation of the late-summer varieties and the root-like couch-grasses. Although the overall cover of the late-summer varieties is essentially unchanged, the covers of certain species are changed. The two most numerous species of the group, *Ambrosia elatior* and *Echinochloa crus-galli*, for example, were reduced to about half compared to their 1950 values, while at the same time *Chenopodium album* and *Amaranthus retroflexus* multiplied appreciably (Table 1).

In contrast with the late-summer varieties, the annual stemmed couch-grasses (G_1) and root-like couch-grasses (G_3) exhibited a considerable decrease as a result of the large-scale agrotechnology (from 5.8% to 1.5% for G_1 and from 16% to 9.3% for G_3), similarly to the results for the wheat crops in 1961 and this year. The greatest decrease now too was for *Convolvulus arvensis*, belonging to group G_3 (from 10.4% to 5.6%). A similar considerable decrease can be observed for *Cirsium arvense*, but in contrast there is an increase for *Rubus caesius* (Table 1).

2. Effect of the application of Atrazin (Hungazin PK) on the development of the weed vegetation in maize crops

a) Weed conditions of maizes sprayed for the first year

On the Enying State Farm 5 kg Hungazin PK and 1.1 kg Dikonirt was applied per kh, and on the other farms 6 kg/kh Hungazin PK (Atrazin) to the maize crops, in the majority of cases on pre-emergents. Application was in all cases performed by aeroplane.

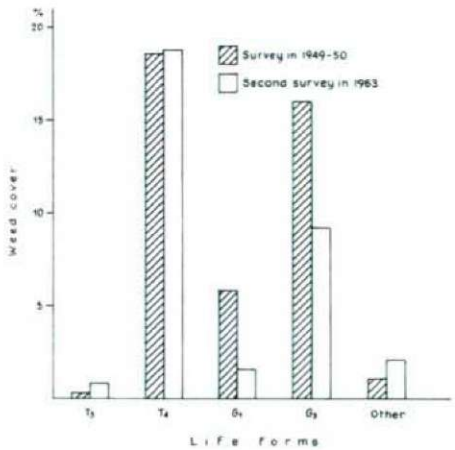

Fig. 2. Effect of large-scale agrotechnology on the cover of the weed groups in maize crops (overall data).

In maizes sprayed for the first time the combined data indicate that Hungazin PK decreased the cover of weeds by about 50% during the complete growing time (Table 2, surveys 1 and 2, and Figs. 3 and 4). In this difference of about 50% in the weed cover of maizes treated with Hungazin, however, it must be remembered that at Enying all of the chemically treated maizes were hoed. At the beginning of

the growing time the difference arising from the hoeing in the average weed cover of these areas (taking into account that the average of several investigation sites is involved) may have been about 0.5—1 %, while at the end of the growing time this difference practically disappeared, since mainly dicotyledonous annuals and geophyte species exhibiting very little or no sensitivity at all to the chemical were weeded out from the crops of the farm, and these soon came up again after the hoeing (see the subsequent paper, and Table 2 and Figs. 3 and 4 there).

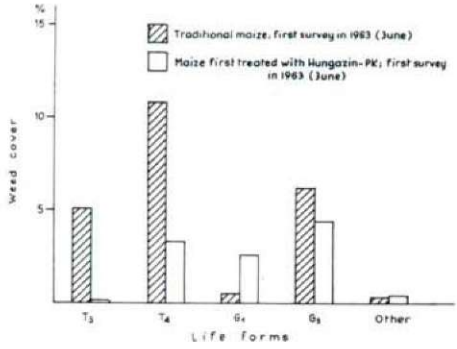

Fig. 3. Effect of Hungazin PK on the weed conditions of maize crops in the first half of the growing period: first-year treatments.

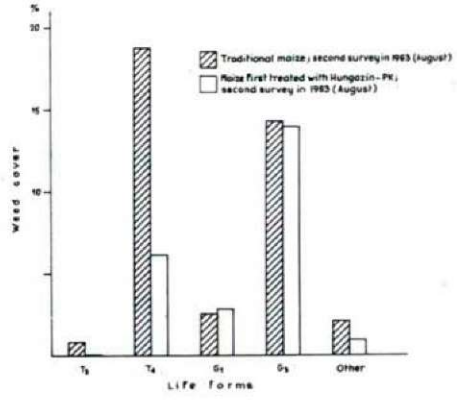

Fig. 4. Effect of Hungazin PK on the weed conditions of maize crops at the end of the growing period: first-year treatments.

It emerges from the data of Table 2 that the Hungazin PK suppressed the spring-sprouting early-summer varieties completely, and the late-summer ones to about one-third during the whole growing time. Of the late-summer varieties, comparatively much *Echninochloa crus-galli* and panic grass *(Setaria)* remained. (This must unconditionally be noted, for this further maintains the contamination of the soils with weed seeds, which may cause a very serious problem in the year of the post-effect. At the same time, the danger remains that as a consequence of selection types of these species more resistant to Hungazin may develop.)

Table 1. More important weed species and % covers in maize crops, based on overall data for examination sites with different treatments

Treatment		Tradi-tional	Traditional		1 yr. Hungazin		2 yr. Hungazin		3 yr. Aminotriazine	
Yeer of survey		1950	1963		1963		1963		1963	
			Surv. I.	Surv. II.	Surv. I.	Surv. II.	Surv. I.	Surv. II.	Surv. I.	Surv. II.
G_1	*Equisetum arvense*	1.58	0.01	1.02			0.64	1.15	3.62	5.47
G_1	*Aristolochia clematitis*	1.00		0.21		0.12				
G_2	*Rubus caesius*	0.72	0.42	1.98	1.47	1.78	1.03	2.74	3.75	6.95
G_3	*Convolvulus arvensis*	10.04	3.89	5.66	1.92	5.21	3.24	9.21	4.35	10.20
T_3	*Sinapis arvensis*	0,13	2.18	0.36	0.07	0.01	0.03	0.01		
T_3	*Raphanus raphanistrum*		2.74	0.18	0.09					
T_4	*Ambrosia elatior*	2.39	1.42	0.91	0.01	0.27	0.05	0.25	0.48	0.94
G_3	*Cirsium arvense*	3.06	1.20	1.08	0.85	1.40	0.53	1.39	0.66	1.13
T_4	*Chenopodium album*	1.83	1.19	3.07	0.25	0.15	0.02	0.01		
T_4	*Amaranthus retroflexus*	0.80	0.62	2.41	0.28	0.31		0.06		
G_1	*Agropyron repens*	0.68	0.11	0.04	2.56	1.70	0.70		0.92	1.00
T_4	*Echinochloa crus-galli*	6.02	3.11	3.09	1.46	3.35	0.21	3.18	1.33	6.50
T_4	*Setaria glauca*	1.55	0.44	1.95	0.20	0.87	0.34	1.21	0.25	1.12
T_4	*Setaria viridis*	1.46	0.52	1.59	0.18	0.71		0.71	0.01	0.09

The weedicide had more difficulty in eliminating the perennials, for the total cover of the varieties wintering in the soil ($G = G_1$, G_2 and G_3) in the first-year treatments agreed with those cultivated by hoeing, or was somewhat larger, throughout the entire growing period. Although as regards the perennials the multiplication of *Convolvulus arvensis* was observed in places, overall its cover did not exceed the value found for the traditionally cultivated crops (Table 1).

b) Development of the weed vegetation in the event of the application of Simazin, Atrazin (Hungazin PK) for several years

Several-year treatments were no encountered at every investigated site. Maize plots sprayed for two years were surveyed at Enying and on the Rózsamajori and Tátomi sub-units of the Kaposvár State Farm. Plots systematically chemically treated for three years were found on the Nagybaráti and Nagykorpádi sub-units of the Lábod State Farm and again at Enying.

Information on the amounts of weedicide applied to the sites investigated is given below:

At Enying the doses applied to the plots treated since 1961 were 5 kg Atrazin in 1961, 1.1 kg Dikonirt in 1962, and again 5 kg Hungazin PK in 1963. Those treated since 1962 received 5 kg Hungazin + 1.1 kg Dikonirt in 1962, and 2.5 kg Hungazin and 1.1 kg Dikonirt in 1963.

On the Lábod State Farm 4.5 and 5 kg Simazin were applied as a basic treatment on 1961 on the Nagybaráti and Nagykorpádi sub-units, respectively, and annually since then 3 kg Hungazin PK.

In the Tátomi sub-unit of the Kaposvár State Farm in 1962 a 4.5 kg Simazin basic treatment was applied, with a 5 kg similar treatment at Rózsamajor; in 1963 a uniform overtreatment of 5 kg Hungazin PK was used at both sites.

The given doses in all cases refer to an area of one cadastral acre (0.57 hectares).

Table 2. Number and % cover of weed species belonging to the individual life forms, as overall averages for the examination sites according to treatments, as found in the surveys for 1950 and 1963

Treatments	Tradnl.		Traditional				1 yr. Hungazin				2 yr. Hungazin				3 yr. Aminotrazine			
Surveys year	1950		1963 I		1963 II		1963 I		1963 II		1963 I		1963 II		1963 I		1963 II	
Species no. (1) % Cover (2)	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Life forms:																		
Annuals																		
T_1	3	0.18	5	0.04	7	0.57			1	0.01			2	0.02	5	0.02	4	0.02
T_2	5	0.21	10	0.05	7	0.35	3	0.03	1	0.01	2	0.01	2	0.02	4	0.02	4	0.02
T_3	5	0.37	6	5.06	8	0.86	3	0.16	1	0 .01	3	0.03	2	0.02	4	0.02	3	0.02
T_4	30	18.58	34	10.81	46	18.76	16	3.32	17	6.16	16	0.79	23	5.82	15	2.22	19	9.86
Total T	43	19.34	55	15.96	68	20.54	22	3.51	20	6.19	21	0.83	29	5.88	28	2.28	30	9.92
Biennials:	1	0.01																
Perennials:																		
H_3	6	0.25	5	0.24	5	0.27	2	0.03	2	0.16	2	0.02	5	0.35	3	0.05	3	0.38
H_5					5	0.86											1	0.01
Total H	10	0.58	5	0.24	10	1.13	2	0.03	2	0.16	2	0.02	5	0.35	3	0.05	4	0.39
G_1	11	5.85	5	0.49	8	1.57	3	2.57	3	1.83	4	1.52	4	1.73	4	5.65	4	7.51
G_2	2	0.15	1	0.02	1	0.06	1	0.36	1	0.74	1	0.11	1	0.33	1	0.35	1	0.31
G_3	11	16.07	7	6.25	10	9.29	6	4.40	6	8.94	6	4.96	7	13.59	6	9.84	6	19.06
Total G.	24	22.07	14	6.76	19	10.92	10	7.33	10	11.51	11	6.59	12	15.65	11	15.84	11	26.88
Overall totals	78	41.99	74	22.96	97	32.59	34	10.87	32	17.86	34	7.44	46	21.88	42	18.17	45	37.19

I: early June survey
II: August survey

1: species no.
2: % cover

T_1 = early-spring hardy annuals
T_2 = autumn-sprouting early-summer annuals
T_3 = spring-sprouting early-summer annuals
T_4 = late-summer annuals

H_3 = tap-rooted
H_5 = oblique-rooted
G_1 = couch-grasses
G_2 = tuberous
G_3 = rhizome-like roots

If the weed cover of maize crops treated with Hungazin over several years is compared with that for the traditionally cultivated crops, one finds somewhat surprisingly that, with the exception of one case, there is no appreciable difference as regards the overall weed cover. This clearly means that even after chemical treatment for 2—3 years maize plots remain weedy; for example, at the end of the growing period in crops sprayed for 3 years (from 1961) the weed cover was higher (37.16%, Table 2, survey 2) than in the hoed crops (32.59%). However, although there are no essential differences in the overall weed covers, very considerable differences can be observed in the distributions of the weed cover according to life-forms, as can be seen from the data of Table 2 and from Figures 5 and 6.

The situation is clearly the same in connection with the annuals as in the first-year treatments, but here appreciably more *Echninochloa crus-galli* remained.

Surprisingly, the perennials wintering in the soil (G) reacted differently to the several-year treatment. Comparison of the survey data reveals that the geophytes (G_1 and G_3) occupied a substantially larger area in the maizes systematically sprayed with aminotriazine than in theose cultivated traditionally. This multiplication can be observed in the crops treated for 2 years (Table 2), but much more so in the regions treated with Hungazin for 3 years, in which the late-summer survey showed the G life-form (G_1 and G_3 together) to have an average cover of 26.88%; this is more than two and a half times the value found in the hoed maizes (10.92%) (Table 2).

In these regions the multiplication of *Equisetum arvense* brought about a 4—5 times greater amount of the couch-grasses (G_1) compared to the traditional values (Table 1). From the group of the root-like couch-grasses (G_3) *Rubus caesius* and *Convolvulus arvensis* showed up in large amounts. Hungazin PK clearly caused no, or only slight damage in these three weeds. This is understandable, since in the majority of cases these species root extremely deeply, and as a result have difficulty in absorbing the root herbicides which act in the upper layer of the soil. Further, an appropriate weedicide effect could not have developed, for in 1963 at Lábod, and at Kaposvár too, the spring was abnormally dry.

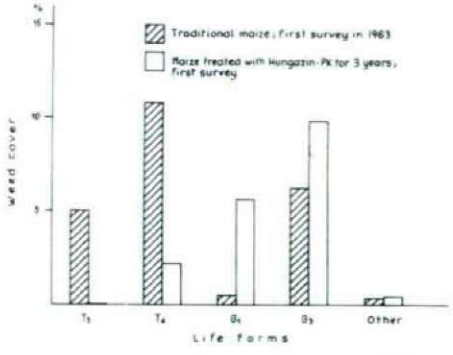

Fig. 5. Effect of 3-year aminotriazine treatment on the distribution of the early-summer weed vegetation in maize plots according to life forms.

Accordingly, although the examination data showed the soils to contain much weedicide, the Hungazin destroyed only the annuals, and of these mainly the very sensitive dicotyledonous ones. Following the destruction of the majority of the

annuals, the conditions temporarily became much more favourable for the deeply-rooted perennials, and to a certain extent for some monocotyledonous late-summer weeds (T_4), including *Echniochloa* and *Setaria* consequently, they gradually took the place of the weed species sensitive to the chemical. In this way the situation arose that in the maizes treated systematically with aminotriazine for several, and particularly 3 years, not only did the overall weed cover not decrease, but it actually increased compared to the state for the traditionally cultivated maizes. Analysis of the weed

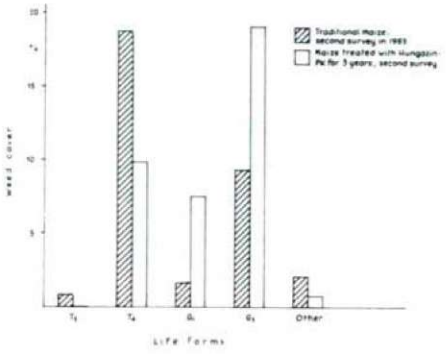

Fig. 6. Effect of 3-year aminotriazine treatment on the distribution of the late-summer weed vegetation in maize plots according to life forms.

cover according to life forms showed that in maizes repeatedly (for 3 years) sprayed with aminotriazine more than two-thirds of the total weed cover (26.88% out of 37.16%) consisted of the most harmful, and most difficult to remove, perennial couch-grasses (G_1) and root-like couch-grasses (G_3); at the same time, the situation is just the reverse in the case of hoeing (cf. Table 2).

As emerged above, therefore, the results of the investigations do not confirm the earlier conceptions of VIRÁG et al. (1962) in connection with this mode of treatment. On the contrary, as a consequence of the one-sided use of Atrazin for a prolonged period the species resistant to this chemical multiply, and the picture which develops on these areas is much less favourable than in the traditionally cultivated plots. Practically simultaneously with the preparation of this manuscript, VIRÁG (1964) also established the multiplication of *Rubus* and *Convolvulus* for such an application of the aminotriazines.

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COMPARATIVE WEED INVESTIGATIONS IN WHEAT AND MAIZE CROPS CULTIVATED TRADITIONALLY AND TREATED WITH WEEDICIDES III. CHANGES IN THE WEED CONDITIONS IN MAIZE PLOTS UNDER SIMAZIN, ATRAZIN (HUNGAZIN PK) POST-EFFECT AND THE DEMONSTRATION OF THE AMINOTRIAZINE CONTENTS OF THE SOILS

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Abstract

In a number of study sites an examination was made of the extent to which the weedicidal effect of the chemical is manifested in the year following spraying, in areas treated with aminotriazines. The aminotriazine contents of the soils were also investigated by biological methods.

The weedicidal action in the year subsequent to spraying was not sufficiently manifested even at the beginning of the growing time, and thus cultivation work became necessary even then; nevertheless, there was a significant weed-cover (70%) compared to the control. *Echinochla crus-galli* appeared in large masses in the areas under the post-effect.

The 5—6 kg/kh basic treatment, and the annual 3 kg overtreatment with Atrazin (Hungazin PK) on the areas systematically treated with aminotriazine for several years should theoretically have been enough to free the maize crops from weeds, and thus the weed-cover was not caused by a deficiency of the chemical.

An appreciable amount of the chemical remains in the cultivation layer in the following spraying with 5—9 kg Hungazin PK, and under suitable conditions this may still result in a certain weedicidal effect at the beginning of the growing time.

Introduction

At the time these investigations were begun (in 1963) it was the generally accepted view that the larger doses (4—6, and even 8 kg/kh) of Simazin, Atrazin (Hungazin PK) used in Hungary were sufficient to maintain maize crops free of weeds in the year following the spraying too, or at most would require one cultivatoring, or possibly a Dikonirt spraying (UBRIZSY, 1960; 1962; SZIGETHY, 1960; 1961; 1963; VIRÁG et al., 1962). At the same time one reference was found suggesting that the weedicide effect was uncertain in the year following the spraying (KACSÓ, 1963). For this reason it seemed advisable to carry out a study of the weed vegetation of maize crops under the first and second year post-effects of the spraying.

Materials and Methods

The investigations were made at the same sites as reported in the first paper of this series. Maize crops under the first year post-effect (sprayed in 1962, but not treated is 1963) were surveyed at all study sites (generally in several sub-units too) with the exception of Lábod, but crops under the second year post-effect (sprayed in 1961) only at Mezőhék and Enying. Information on the con-

ditions and method of survey, and on the aspects of the compilations of the tabulated data, is given again in the first paper (FEKETE, 1973).

The weedicides and their doses applied in 1962 to the areas now under the first year post-effect are listed in Table 1. (There were plots in both sub-units of the Mezőnagymihály State Farm, and these received 6 or 9 kg weedicide.)

The same doses were applied to the areas under the second year post-effect (sprayed in 1961): at Mezőhék 5 kg Simazin, and on some plots Atrazin, and at Enying 5 kg Atrazin per cadastral acre (0.57 hectares). In the latter farm the area also received a Dikonirt spraying (1.1 kg/kh) in 1962.

Information on the times, means and method of weedicide treatment is given below.

All of the maizes under post-effect at Fehérgyarmat, on the Klementina sub-unit of the Mezőnagymihály State Farm, and at Enying received two, and at Kaposvár three mechanical and one manual row-hoeing, while on the Bagjas sub-unit of the Mezőnagymihály State Farm they were cultivatored only twice. The plots at Mezőhék under post-effect underwent the traditional treatment: three mechanical and two manual row-hoeings. By the time of the first surveys the crops at Mezőhék and Enying had received one hoeing over the entire area, the former directly before the surveys. and the latter 2—3 weeks earlier. Cultivatoring had also been carried out on the other farms 2—3 weeks before the first surveys. The second cultivatoring and row-hoeing took place immediately after the first surveys.

The method used to demonstrate the amount of the chemical remaining in the soil was the *Sinapis alba* germination test devised by VIRÁG et al. (1960). For this purpose the soils were in all cases collected in 10 cm layers from 0 to 40 cm. 10 samples were taken from each layer. An average sample was prepared by mixing the 10 samples, and 100 seeds of *Sinapis alba* were planted in each mixed soil in large Petri dishes. The germination was carried out in a greenhouse at 20 ± 2 °C, in 3 repetitions. The percentage loss of the seedlings used in each test refers to the 15th day. Germination in soils from the same collecting site, but not treated chemically, and on wet filter paper served as control: the germination capacity of the mustard seed in these cases was 95—97%.

Results and discussion

1. Change of the weed conditions in maize crops under aminotriazine post-effect

a) Weed cover of crops under first year post-effect

It can be seen in Table 3 and Figs. 1 and 2 that in the crops under the first year post-effect of Hungazin treatment, but not treated in the year of the investigation, in spite of the agrotechnical procedures employed a significant restoration of

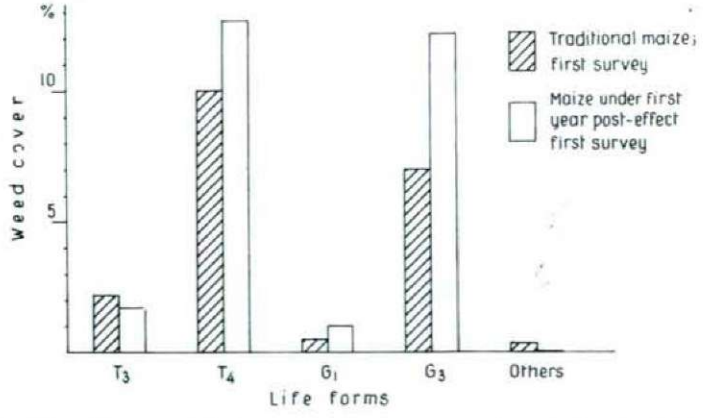

Fig. 1. Distribution according to life forms of early-summer weed vegetation in maize crops under first year Hungazin PK post-effect.

the weed situation had proceeded, for the average weed cover by the end of the growing time had increased by about 70% compared to that in traditionally cultivated maize plots. Fortunately, this unfavourable picture was not completely general. For example, the weed cover of the maizes under the first year post-effect at Mezőhék and Enying were relatively satisfactory. In contrast, from the beginning of the growing time on, the post-effect maize crops on the Fehérgyarmat, Mezőnagymihály and Kaposvár State Farms were characterized by a huge increase in the weed cover, which was naturally further enhanced until the autumn.

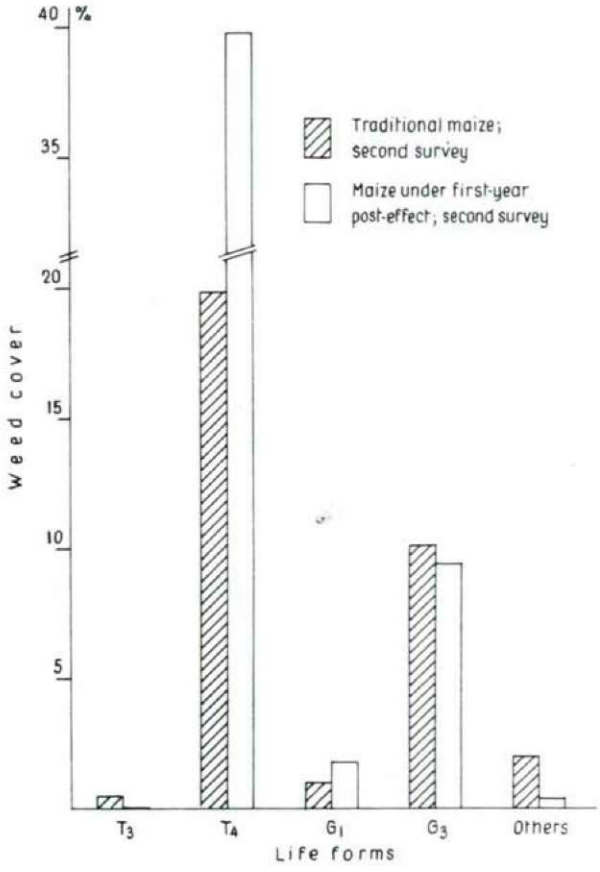

Fig. 2. Distribution according to life forms of late-summer weed vegetation in maize crops under first year Hungazin PK post-effect.

Examination of the composition of the weed vegetation revealed a particularly striking increase in the late-summer varieties (T_4), and primarily *Echinochloa crus-galli*, mainly on the last-mentioned farms. It can be conceived to what extent this took place, for instance, for ripening at the end of summer on the Bagjas sub-unit of the Mezőnagymihály State Farm it attained a 32% cover in the dry state. This enormous weed mass ripened and disseminated an unbelievable amount of seeds,

and hence contaminated the soil for years. The mass appearance of *Echinochloa* in the wheat crops of the farm under Simazin post-effect can also certainly be attributed to the fact that a similarly large amount may have occurred in the maize crops under first year post-effect in the previous year (FEKETE, 1964; 1973). Such a large-scale multiplication of *Echinochloa* was also observed on the Fehérgyarmat and Kaposvár State Farms. In contrast, this phenomenon could not be perceived at all at Mezőhék and Enying.

The root-like couch-grasses (G_3) similarly appeared with higher covers in maize crops under the post-effect, than in those cultivated traditionally; this increase in the weed cover was mainly due to *Rubus caesius* and *Convolvulus arvensis*.

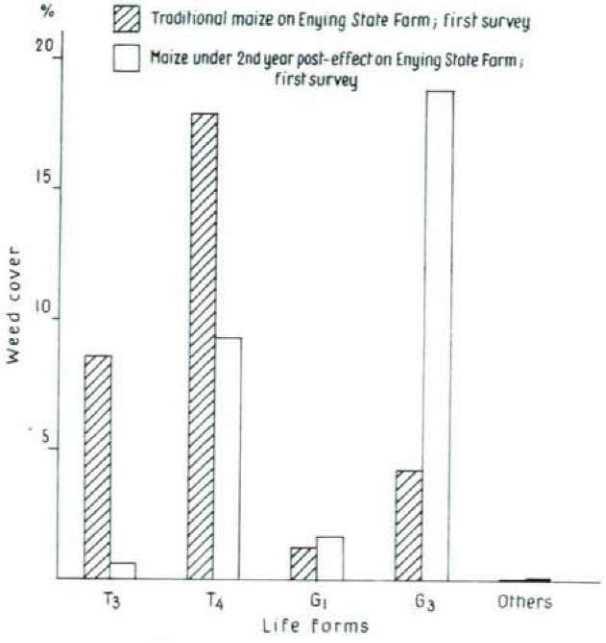

Fig. 3. Distribution according to life forms of early-summer weed vegetation in maize crops under second year Atrazin post-effect on the Enying State Farm.

In the present case, therefore, the data of the surveys do not support the earlier findings; thus, the weedicide effect had not materialized sufficiently at the beginning of the growing time in the maize plots treated with aminotriazine in the previous year, and accordingly hoeing had become necessary everywhere. But even so, despite the additional hoeing, there was a massive accumulation of *Echinochloa crus-galli* in places (3 farms, 5 sub-units). At the same time the maizes at Mezőhék and Enying were comparatively good, their weed covers being somewhat less than in the traditionally cultivated crops, but naturally, as already mentioned, agrotechnical procedures were also applied in these to eliminate the weeds.

Although the weedicide effect did not prove satisfactory, nevertheless the action of the chemical could be seen in the early-summer weed cover: great reductions could be observed in the sensitive dicotyledonous species, and indeed, on the application of large doses (9 kg/kh), in the monocotyledonous species too.

b) Weed cover of crops under second year post-effect

The data of the weed covers of the crops under the second year post-effect are comprised of the data from the surveys of an almost completely clear area (at Mezőhék, weed cover 0—13%) and a fairly weedy area (at Enying, weed cover 30—52%). Naturally, this is not reflected in the averages. This calculation was carried out only for the sake of uniformity. More information is given in Table 4 and Figs. 3 and 4 with regard to the more important weeds in these crops at Enying.

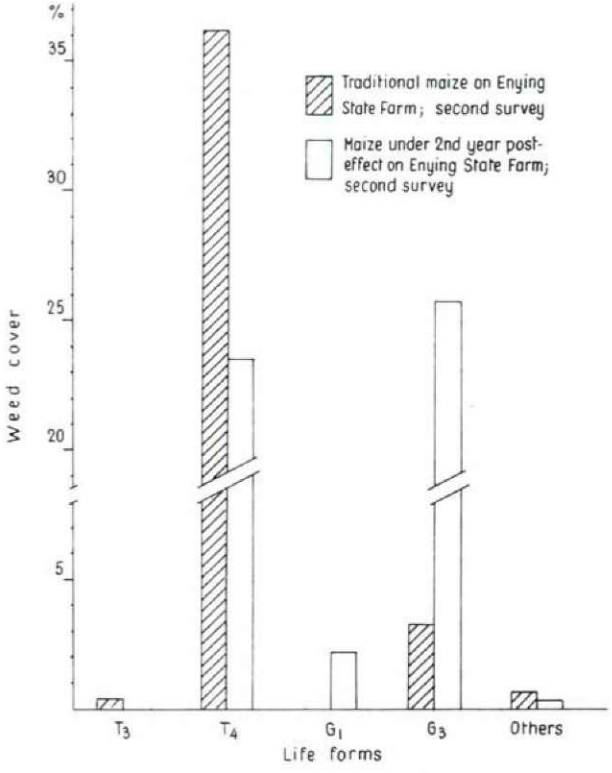

Fig. 4. Distribution according to life forms of late-summer weed vegetation in maize crops under second year Atrazin post-effect on the Enying State Farm.

It is clear from the data of Table 3 that the total weed covers of these areas did not attain the levels in the hoed crops. In fact, however, the clearing of the soil was observed only at Mezőhék, where the crops received exactly the same number of hoeings as the traditionally cultivated crops. At Enying, on the other hand, because of the lack of the post-effect the applied treatment (two mechanical and one manual hoeing) proved insufficient, and there was an appreciable weed cover in the crops. Here the perennials which had multiplied in the previous year (*Rubus* and *Convolvulus*) as a result of the chemical treatment, together with the newly appearing annuals (T_4), comprised a larger weed mass (52%) than in the untreated areas.

2. Demonstration of the aminotriazine content of the soils by a biological method

One of the reasons for the determination of the weedicide content of soils treated with Simazin or Atrazin (Hungazin PK) was to obtain an answer to the question of whether there is a difference between the autumn and spring sprayings as regards the utilization of the chemical, and its washing-down into the deeper layers of the soil. Other questions were whether the amount of weedicide applied was sufficient in the case of crops over-treated with Hungazin for several years; and whether the soils of the areas under post-effect still contain any of the chemical at all, considering the extensive weeding-up of the maize crops.

Table 1. Weedicides applied in areas under first year post-effect (sprayed in 1962)

Studi sites	Dose applied per kh in 1962	
Fehérgyarmat	5 kg 2.5 kg	Simazin-1961 Hungazin PK
Mezőnagymihály	6 kg 9 kg	Hungazin PK Hungazin PK
Mezőhék	4.6—5 kg	Hungazin PK
Enying	5 kg 1.1 kg	Hungazin PK + Dikonirt
Kaposvár	5 kg	Simazin

On the occasion of survey 2 (autumn) to decide the above questions, soil samples were taken from the chemically treated maize crops, and under the post-effect, and the weedicide contents of these samples were determined with the *Sinapis alba* test, as described under "Methods".

a) Comparison of weedicide contents of soils sprayed in autumn and in spring

The examination data show that in the case of the automn spraying the weedicide is not washed down into the deeper layers of the soil, not even as a result of the significant winter precipitation: the percentage loss of the *Sinapis alba* at the end of the growing time in the soil of maize sprayed in the autumn was roughly the same (and even a little higher) than the corresponding value for the spring spraying (84% and 75—76%, respectively).

As regards the decomposition or utilization of the chemical, or its washing-out from the cultivation layer there is no difference between the autumn or spring sprayings with Hungazin; in principle, therefore, approximately the same weedicide effect can be reckoned with in the two cases.

Table 2. More important weed species and their % covers in maize crops under Hungazin post-effect, compared with traditionally cultivated crops at the same study sites (overall data)

Treatment	Traditional		1st year Hungazin post-effect		2nd year Aminotriazine post-effect	
Survey	I	II	I	II	I	II
G_1 *Equisetum arvense*		0.73	0.12	0.35	0.56	1.00
G_3 *Rubus caesius*	0.49	2.64	2.55	4.99	5.86	8.13
G_3 *Convolvulus arvensis*	4.27	5.46	7.62	7.86	3.51	4.24
T_4 *Hibiscus trionum*	0.27	1.35	1.32	2.46	0.12	3.31
T_3 *Sinapis arvensis*	2.19	0.09	1.25	0.02	0.30	0.04
G_3 *Lepidium draba*	0.23	0.08	1.01	0.15		0.01
T_4 *Ambrosia elatior*	0.69	1.72	0.27	0.94	2.73	5.63
G_3 *Cirsium arvense*	1.44	1.57	0.98	1.78	0.01	2.19
T_4 *Chenopodium album*	1.37	3.72	0.25	1.82	0.09	0.70
T_4 *Amaranthus retroflexus*	0.77	2.49	0.15	3.54	0.01	0.94
T_4 *Digitaria sanquinalis*	0.02	0.58	0.02	1.00		
T_4 *Echinochloa crus-galli*	2.57	3.31	5.99	20.18	0.09	0.17
T_4 *Setaria glauca*	1.44	2.15	0.65	4.13	0.23	1.13
T_4 *qetaria viridis*	0.22	1.08	2.58	4.40	1.21	3.33

Table 3. Numbers and % covers of weed species belonging to the individual life forms as overall averages for the study sites according to treatments

Treatment	Traditional				1st year Hungazin post-effect				2nd year Aminotriazine post-effect			
Survey	I		II		I		II		I		II	
Species no. (1) % Cover (2)	1	2	1	2	1	2	1	2	1	2	1	2
Life forms: Annuals												
T_1	2	0.01	9	0.27	3	0.01	5	0.17				
T_2	7	0.02	5	0.07	3	0.03	5	0.05			1	0.01
T_3	4	2.23	5	0.50	6	1.73	7	0.18	2	0.31	2	0.04
T_4	38	10.00	45	19.86	28	12.69	33	39.79	14	4.68	14	16.86
Total T	51	12.26	64	20.70	40	14.46	50	40.19	16	4.99	17	16.91
Biennials							2	0.01				
Perennials												
H_2			1	0.08								
H_3	4	0.31	4	0.35	2	0.01	3	0.14	2	0.01	2	0.14
H_4							1	0.01				
H_5			3	1.17			1	0.01				
Total H	4	0.31	8	1.60	2	0.01	5	0.16	2	0.01	2	0.14
G_1	5	0.54	10	1.00	5	0.98	6	1.80	2	0.87	3	1.12
G_2	1	0.02	1	0.06	1	0.04	1	0.05	1	0.04	1	0.06
G_3	9	6.95	10	10.12	7	12.22	6	14.82	4	9.38	5	14.56
Total G	15	7.50	21	11.18	13	13.24	13	16.67	7	10.29	9	15.74
Overall totals	70	20.07	93	33.48	55	27.71	70	57.03	25	15.29	28	32.79

b) Weedicide contents of maize soils treated with Simazin or Atrazin (Hungazin PK) for several years

The percentage loss of the test plant (90—100%) in the soils of the areas systematically treated with aminotriazine for 2—3 years indicated that the 0—10 cm layers of these soils, and at Lábod even the 10—20 cm layer too (80% loss), contained very much weedicide.

Accordingly, the chemical content of the soil, after the application by spraying for 2—3 years of the amounts of weedicide given in the first paper, should theoretically be sufficient to free the maize crops from weeds. The fact that in spite of the high chemical content of these soils they were nevertheless weed-infested can be attributed to two factors: in the areas under consideration species resistant to aminotriazines predominated, and the amount of precipitation which fell in the spring months was not enough for the weedicide to exert its effect.

From the satisfactorily high chemical content of the soils, therefore, only the destruction of the weeds sensitive to aminotriazine can be expected, and the weedicide effect can be exerted only in the event of the sufficient moistness of the soil.

Table 4. Percentage covers of more important weeds in maize crops of Enying State Farm under traditional and second year Atrazin post-effects

Treatment	Traditional		2nd year Atrazin post-ffect	
Survey	I	II	I	II
Equisetum arvense			1.12	1.99
Rubus caesius		0.64	11.72	15.00
Convolvulus arvensis	2.83	2.23	7.03	8.12
Hibiscus trionum		0.01	0.25	2.87
Sinapis arvensis	8.54	0.39	0.61	0.06
Ambrosia elatior	4.16	10.34	5.46	11.25
Cirsium arvense	1.10	0.42	0.02	2.56
Chenopodium album	5.97	10.03	0.18	1.39
Amaranthus retroflexus	2.91	9.01		0.01
Amaranthus blitoides	1.12	2.07		
Polygonum convolvulus	0.89	1.31	0.02	0.46
Setaria glauca		0.03	0.47	2.26
Setaria viridis	1.34	2.09	2.42	4.18

c) Weedicide contents of maize soils under the post-effect

16—18% of the *Sinapis alba* died in samples taken from the 0—10 cm soil layers at the end of the growing period in the year (1963) following the spraying, in the areas under the first-year post-effect of the application of 5—6 kg Hungazin PK (in 1962). The test plant did not die in the soil samples taken from the 10—20 cm layers, but the yellowing at the edges of the cotyledons indicated that this depth of soil does contain a small amount of weedicide.

On the application of doses of 9 kg per cadastral acre (the Klementina and Bagjas sub-units of the Mezőnagymihály State Farm), a 42—45% plant loss was observed in the 0—10 cm soil level; this points to a still considerable chemical content. Indeed, in the 10—20 cm level *Sinapis* losses of 20 and 34% were observed at Klementina and Bagjas, respectively. (At Klementina the chemical was applied in 2 parts: 6 kg in the autumn of 1961 and 3 kg in the spring of 1962, while at Bagjas the total amount was sprayed in one application, in the spring of 1962.)

The data thus show that an appreciable amount of the chemical remains in the cultivation layer even in the second year after the application of the weedicide, and under appropriate conditions this chemical content can result in a certain weedicidal effect. This is shown by the weed coenological surveys at Enying, at Mezőhék, and to a certain extent on the 100 sub-unit of the Fehérgyarmat State Farm at the beginning of the growing period. It is unfortunate that it was precisely on the Mezőnagymihály State Farm, where very large doses were used, that a weak weedicidal effect was exhibited in the second year.

Aminotriazine could not be detected from any of the soil levels examined by the biological method at the end of the growing period in 1963, on the areas under the second year (1961 spraying) post-effect. It seems that by the third year following the application of chloraminotriazine the chemical has already been consumed, decomposed or washed out of the cultivation layer. This conclusion is fully supported by the results of the studies relating to the weed cover.

As mentioned in the first paper (Fekete, 1973), a study prepared in the spring of 1964 (within the framework of one paper, following a treatment according to farms) contained the material of the three parts of the Hungarian Academy of Sciences at that time under the pressent title. but unfortunately could not then be published. For this reason. certain of the problems and results discussed in three papers must be considered in the light that nearelly a decade has passed since these were written,

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ULTRASTRUCTURE AND MECHANISM OF SECRETION IN EXTRAFLORAL NECTARIES OF RICINUS COMMUNIS L.

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Abstract

Electronmicroscopic examinations of the cells of the extrafloral nectary of *Ricinus communis* L. were used to study the question of whether the nectar transport is a granulocrine process linked to a cell-component, or the result of molecular transport.

It could be concluded from the results that the fluid transport is a function of the lomasomes: there are many in the grandular tissue cells of the functioning nectary, and there are many mitochondria around them. The cell wall accumulating role of the lomasomes is not probable, since they can be found only in functioning glandular tissue cells, and significant wall-building processes can not be observed in the period of secretion.

To date the study of the relation between the fine structure and function of the nectaries has been dealt with by many research workers, e.g. MERCER and RATHGEBER (1962), WHRISCHER (1962), SCHNEPF (1964a, b), EYMÉ (1966a, b, 1967), VASILIEV (1969), FAHN and RACHMILEVITZ (1970), FINDLAY and MERCER (1971), VASILIEV (1971) and RACHMILEVITZ and FAHN (1973).

In spite of this, there are at present a fair number of conceptions as to the mechanism of nectar secretion. Nor has the important question been clarified as to the nature of the cell organelle to which the fermentative transformation of the sugars, for example, and the nectar transport are linked.

In our work we have studied the ultrastructure of the extrafloral nectary to establish whether the transport is a granulocrine process related to a cell component, or whether the phenomenon of molecular transport occurs.

Studies to date indicate the presence of well-developed ER in the nectarogenous cells. MERCER and RATHGEBER (1962), SCHNEPF (1964a, b), and FAHN and RACHMILEVITZ (1970, 1973) have suggested the possibility that vesicles of reticular origin might take part in the transport of the sugary fluid.

EYMÉ (1966a, b, 1967) and FINDLAY and MERCER (1971) have described multivesicular structures from the secreting nectaries. EYMÉ conceived that the sugar is secreted as a fluid via vesicles of Golgi origin.

A very recent paper (RACHMILEVITZ and FAHN 1973) takes into account the previous findings and concludes that the sugary fluid is secreted by vesicles of ER origin.

Another type of conception is transport by molecular means. As a result of his observations, SCHNEPF (1964a, b) reached the conclusion that the plasmalemma is the site of localization of enzymes and carriers which assist the transport of sugar molecules across the membrane.

According to VASILIEV (1969), the protoplasm of the cells does not take part directly in the transport of the bulk of the nectar. Part of the phloem fluid proceeds passively in the cell wall, and part by means of an active transport mechanism in the protoplasm.

Materials and Methods

Segments from the individualt issue areas from the extrafloral nectary of *Ricinus communis L.* in various stages of ontogenetic development were fixed in 3% glutaraldehyde. After the 3-hour fixation, the tissue pieces were washed in phosphate buffer and postfixed in 1% buffered OsO_4. The material was dehydrated in ethanol and embedded in Durcupan ACM.

The ultrathin sections were stained with uranyl acetate and lead citrate, and examined with TESLA 242 D and JEM 100 B electronmicroscopes.

For the light-microscopic examinations the nectaries were embedded in celloidin.

Observations

The automorphic extrafloral nectaries of ricinus develop at the two ends of the leaf-stalk, in the vicinity of the base and leaf-plate. Viewed from above they resemble an elongated disc. *Ricinus* is one of those rare plants in which the nectaries also appear on the cotyledon.

The glands vary as to number and site of occurrence. They generally occur singly on the lower part of the leaf-stalk, whereas one or two large glands may develop near the plate.

Our histogenetic examinations show that the nectary is formed completely before the final development of the leaf-plate and leaf-stalk.

From a structural aspect the nectary consists of two important tissue regions: glandular tissue and parenchyma.

Thick cuticle covers the epidermal cells over the nectary. The epidermis covering the glandular tissue consists of column-shaped cells. Among these it was also possible in places to observe ducts covered by cuticle. The ducts are interconnected with the small intercellulars between the epidermis and glandular tissue, where the nectar is preliminarily collected after secretion from the glandular tissue.

The small-cell glandular tissue is surrounded by parenchyma, in which mainly calcium oxalate and starch accumulate. Vascular bundles consisting of yxlem and phloem elements run into the parenchyma from the leaf-stalk in the direction of the glandular tissue. Before they reach the vicinity of the glandular tissue they are richly ramified. The tracheal and tracheidal lines finally continue into xylem parenchyma. The terminal branches of the phloem part run directly up to the glandular tissue. From here the phloem fluid is transferred to the glandular tissue cells by cells of a "transfusion" nature.

Ultrastructure of nectary cells in the stage of secretion

In the study of the fine structure we paid the greatest attention to the structure of the glandular tissue cells, since it is to this tissue region that the transformation of the phloem fluid and the secretion of the nectar are attributed.

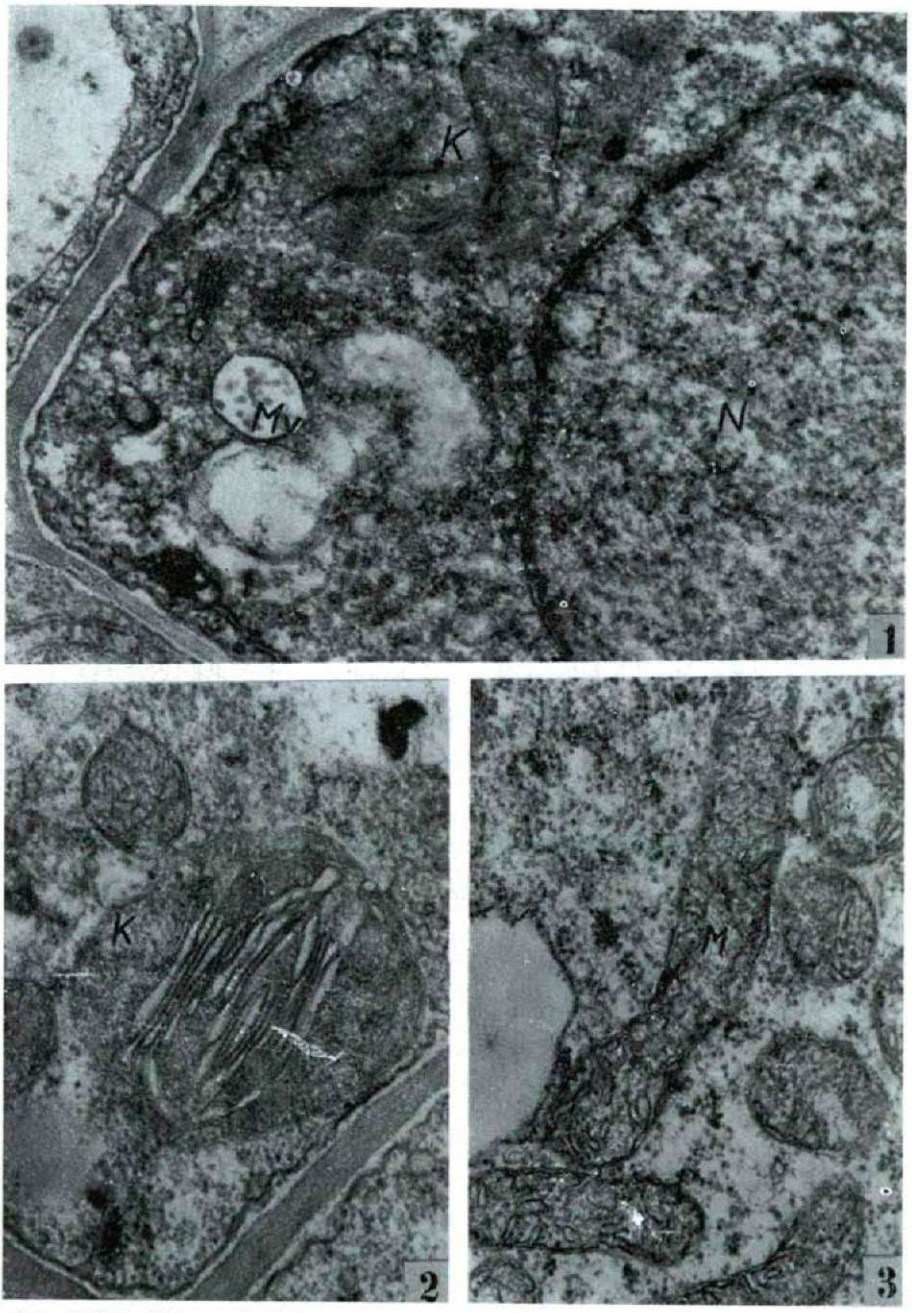

Fig. 1. 1. Cell detail from glandular tissue. The closeness of the multivesicular bodies to the Golgi apparatus points to their possible origin (x27 000).
2. Chloroplast cross-section from the phase of maximum secretion (x34 000).
3. The number of mitochondria correlated with the secretory activity is very high (x34 000).

Light-microscopically, this consists of isodiametric cells. At the beginning of secretion the cytokar ratio in these cells is 1:1, while later the amount of cytoplasm dominates.

The ricinus nectary cells are only relatively rich in granular ER, in contrast with the floral nectaries, where hyperactive agranular or granular ER has been observed by the above-mentioned authors. In ricinus a real lacunar system develops at several places between the membranes of the reticulum, the cisternae are distended, and the isolation of smaller vesicles is common.

Mono- and polyribosomes can be seen in large numbers in the cytoplasm.

There are few chloroplasts; they vary in size in the range 3—4 μ and are ovate, but are frequently deformed. The lipoprotein lamellar system is condensed in the central part of the granular stroma. The grains comprise 2—5 grana vesicles. The strach grains (8—10) can be found near the poles of the chloroplasts. The weakly developed lamellar system is indicative of minimal photosynthetic activity (Fig. 1,2).

The mitochondria are very varied in shape. Besides the elongated form, it is also possible to observe U, Y and ramified forms too. Their length is generally 1.8—2.4 μ, and there are very many of them in the secretory glands (Fig. 1,3).

The Golgi apparatuses are localized near the vacuole-system of the cells, and sometimes in the vicinity of the multivesicular bodies. Similarly as indicated by the observations of FAHN (1970), their number is not indicative of high activity. They may participate in the secretion, but because of their low occurrence their role in the transport processes is difficult to conceive (Fig. 1,1., Fig. 2,3).

Multivesicular bodies were also observed in the ageing, and no longer secreting nectaries. The diameters of these is 0.5—0.7 μ; their role in the secretion has not yet been elucidated. Their closeness to the Golgi apparatus points to their possible origin. A large number of vesicles of dense content can be seen within the membrane (Fig. 1,1).

The wall of the glandular tissue cells consists exclusively of cellulose. According to the literature data published so far, this tissue is without intercellular. Microphotographs reveal that on the meeting of cells (in a functioning gland) intercellulars with loose structure are found in all cases. In the course of the gradual ageing of the nectary this spongy structure becomes increasingly broken up, and lacunae develop in it.

In the peripheral and central parts of the cytoplasm a strikingly high number of large-volume lomasomes were observed (Figs. 2—3). On the sectional surface of one cell there are 5—6 lomasomes, occupying a very large volume compared to the amount of the cytoplasm. This observation holds for all glandular tissue cells. It should be noted that lomasomes were not observed in non-functioning glands. These organelles are present in the part of the cytoplasm near to the nucleus, just as the vicinity of the plasmalemma. Taking into consideration a picture (Fig. 2,1) showing vesicles crossing the plasmalemma, it seems justified to assume that in the present case the lomasomes take part not in the accumulation of the wall material (as is beginning to receive general acceptance), but in the nectar transport. The vesicles of the lomasomes contain dense material. The closeness of these organelles to the mitochondria and ER is striking. It can be seen in Fig. 3,3 that the ER closely adheres to the external membrane of the lomasome. Between the larger vesicles, which probably contain phloem fluid, small vesicles can be observed, similar in size to the diameter of the reticulum. All this permits the conclusion that those fermentative processes which result in a sugar composition characteristic of ricinus

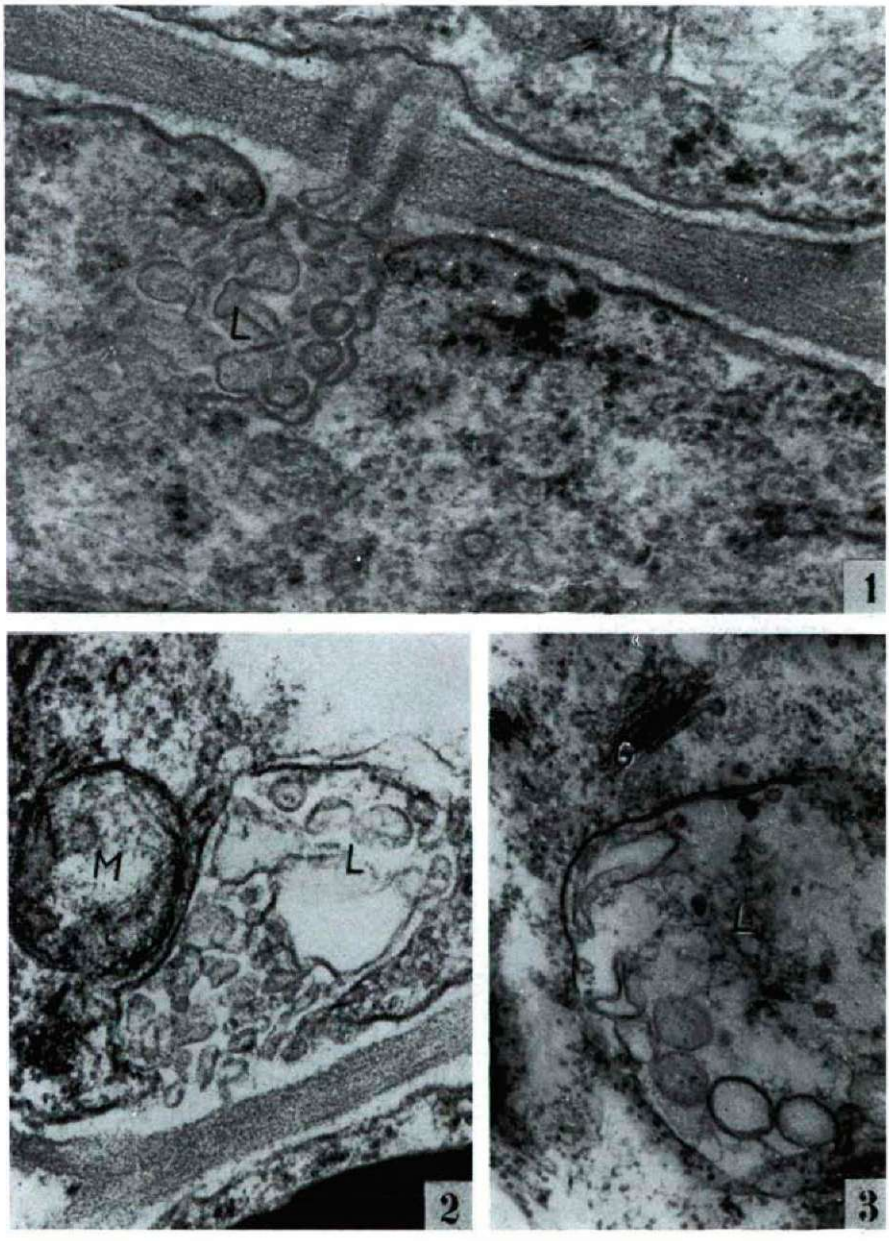

Fig. 2,1. The vesicles of the nectar-transporting lomasomes cross the plasmalemma (x74 000).
2. The energy necessary for the fermentative processes in the lomasomes is provided by the mitochondria (x39 000).
3. Lomasome and Golgi apparatus (x35 000).

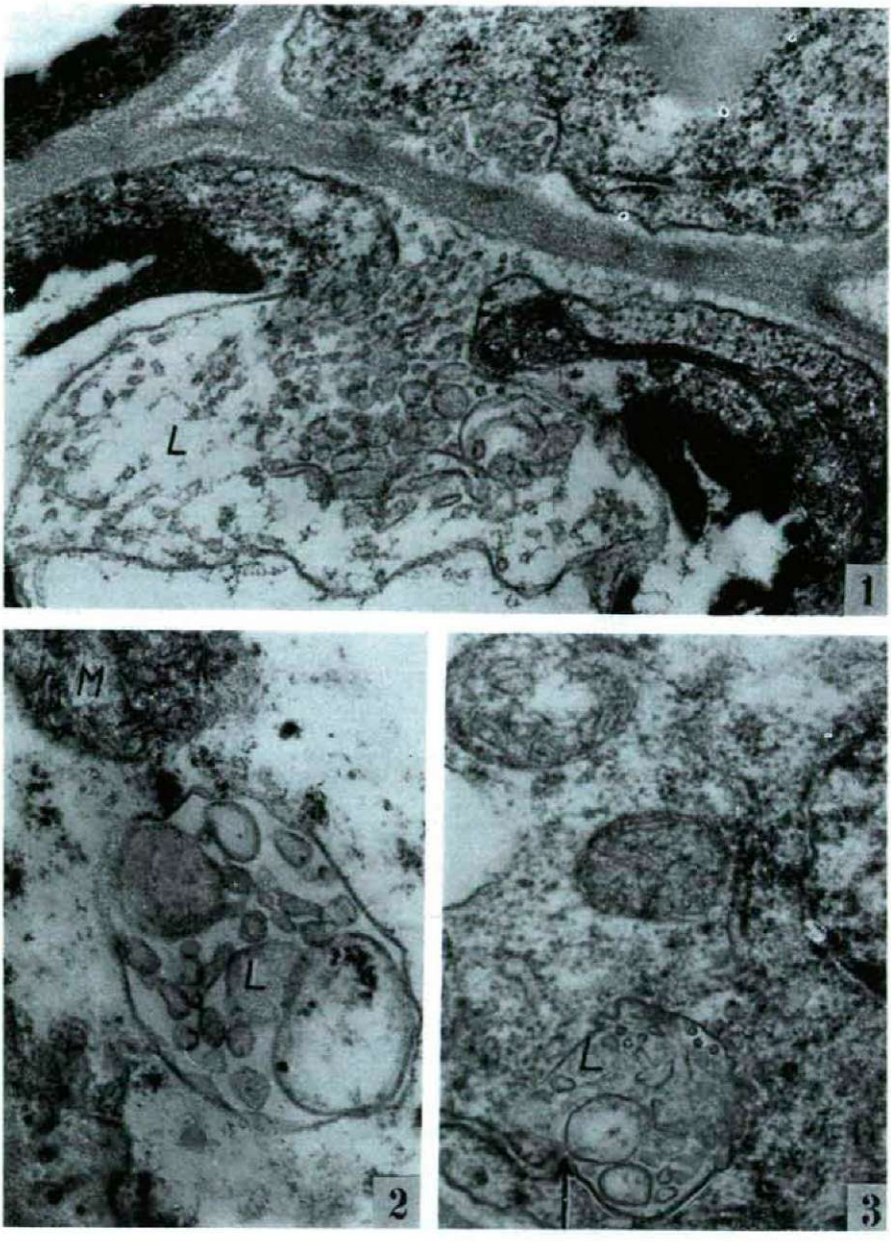

Fig. 3,1. The lomasomes take part not in the accumulation of the wall material in the cells, but in the nectar transport. For a possible minimal wall-material accumulation the participation of the lomasomes with such a significant volume is not considered necessary (x39 000).

2. 43 000x.

3. Vesicles similar in size to the ER diameter between the vesicles of the lomasome. A close connection of the ER can be observed (arrow) (x35 000).

nectar from the phloem fluid, take place within the lomasome. The energy necessary for the processes is provided by the mitochondria in the vicinity of the reaction.

The secretory surface of the nectary:

The ultrastructure of the column-shaped epidermal cells covering the gland agrees essentially with the fine structure characteristic of the glandular tissue. The only difference appears in the vacuolization. Numerous small vacuoles can be seen in the peripheral cytoplasm, while the central ones are fused into one central vacuole (Fig. 4,4).

The surface of the columnar epidermal cells is covered by very thick (5 μ) cuticle. Light-microscopic examinations showed that ducts bounded by cuticle also occur between the columnar epidermal cells, and we assume that the bulk of the nectar may reach the surface via these.

Electronmicroscopic examinations supported the above findings. The ducts run to the surface and there broaden out like a funnel. Their content is osmiophilic, and this can be observed continuously under the cuticle covering the epidermal cells.

Ultrastructure of nectaries in period following secretion

A considerable change occurs at the organelle level in the structure of the glandular tissue cells in the period following secretion. Deep cavitation proceeds on the surface of the nucleus, its shape is extended and it exhibits varied forms. Chromatin may accumulate in aggregates in the karyoplasm (Fig. 4,1).

Vacuolization of the cytoplasm is enhanced. The presence of autophage vacuoles is also indicated by ZIEGLER (1968) and VASILIEV (1971). Cytoplasm, ER and ribosomes can be observed in the autophage vacuole shown in Fig. 4,1. The amount of ER decreases, and the membranes are frequently fragmented.

The originally ovate chloroplasts flatten out, but their lamellar system is substantially more developed than in the previous stage, while the number of grains increases by a factor of 3. Moniliform lipoid drops are secreted below the peristromium (Fig. 4,1). The gland now obtains the greater part of the carbohydrates necessary for its vital processes not via the sieve elements, but by producing them during the photoreactions (Fig. 4,3).

The appearance of the peroxysomes is striking (Fig. 4,2), which indicates that the functions are changed in the nectarogenous cells.

The Golgi apparatus does not exhibit a numerical decrease, while in addition to the cisternae vesicles with a dark content can be seen.

The cell wall is not thickened even in the aged state. Lacunae develop from the loose-structured intercellulars of the secretory glandular tissue.

There are fewer mitochondria and chloroplasts in the parenchyma cells of the nectary. The cytoplasm forms a thin layer along the cell wall. The major part of the volume of the cells is comprised of the coherent vacuole system. The cell wall layers separate from each other in several places. By the end of the secretion period the plasm of the parenchyma cells, originally fulfilling a storing role, is contracted, its place being taken over by the ever larger vacuoles.

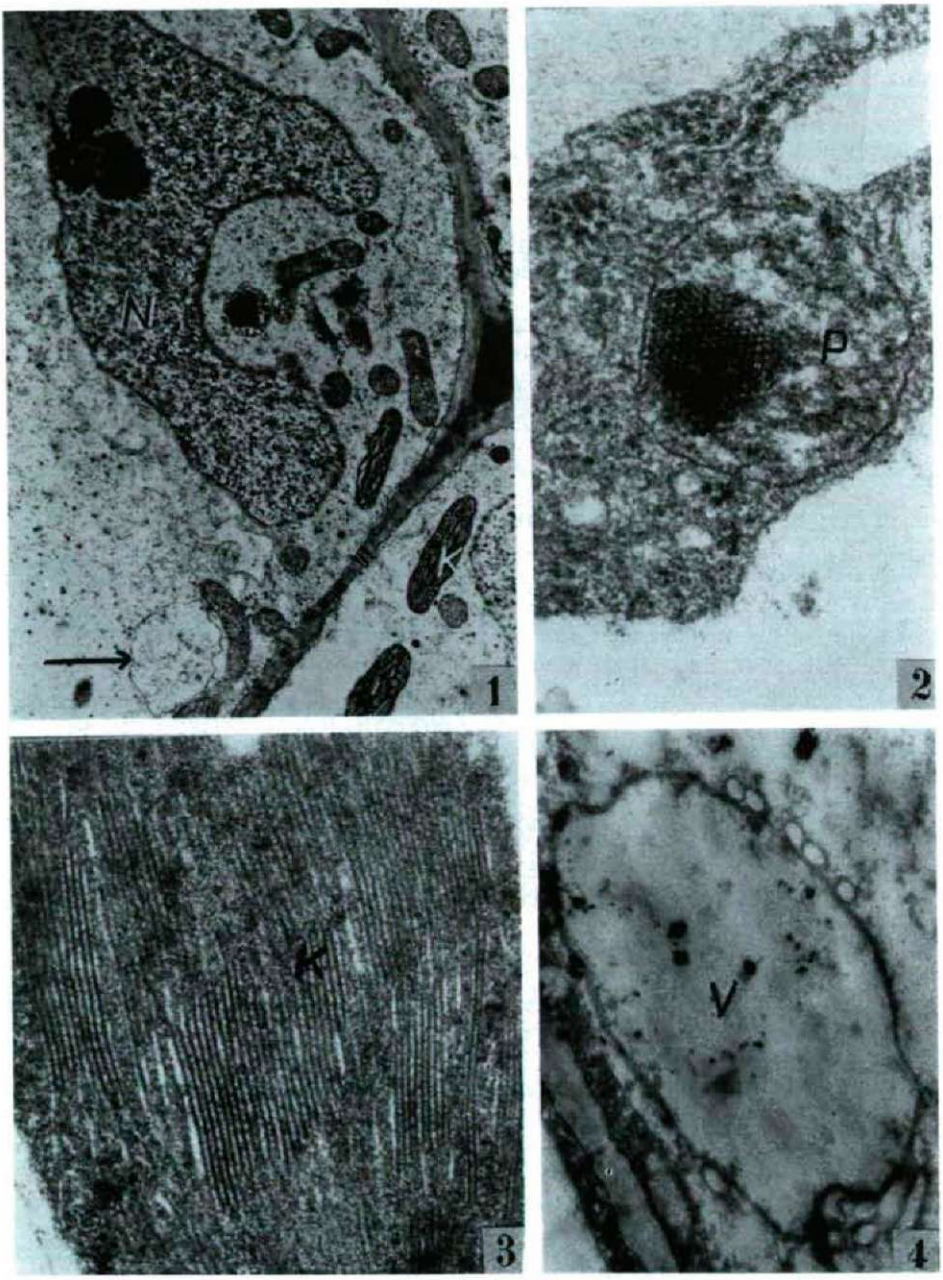

Fig. 4,1. Glandular tissue cells in the period following secretion. Autophage vacuoles appear in the cytoplasm (x20 000).
2. Peroxysome from grandular tissue cell (x56 000).
3. The lamellar system of the chloroplasts is more developed (x60 000).
4. Detail from columnar epidermal cell, with vacuole (x20 000).

Discussion

By examining the ultrastructure of the extrafloral nectaries of ricinus, we tried to find an answer to the question of whether the nectar transport is a granulocrine process linked to a cell component, or proceeds by molecular transport.

There is, practically unanimous agreement (MERCER and RATHGEBER, 1962; WHRISCHER, 1962; SCHNEPF, 1964a, b; EYMÉ, 1966a, b; 1967; VASILIEV, 1969, 1971; FAHN and RACHMILEVITZ, 1970, 1973; FINDLAY and MERCER, 1971) that the most highly developed organelles in the cells of the various nectaries are the mitochondria and ER.

In physiological examinations, ZIEGLER (1955) found that the respiration of the nectaries is very intensive in the period of secretion. This was confirmed by electronmicroscopic examinations. These observations led MERCER and RATHGEBER (1962), SCHNEPF (1964a, b) and FAHN and RACHMILEVITZ (1970, 1973) to conclude that the ER somehow fulfils an important synthetic and transport function. These authors generally studied floral glands. In such glands, however, it is necessary to reckon with many factors which are not involved in the functioning of extrafloral glands. Thus, the development processes of the seed and ovary, the steroid synthesis assumed by VASILIEV, and possibly the enzyme demands of these processes may be interrelated with the high development of the ER.

The functioning of the extrafloral glands can be regarded as somewhat more simple.

EYMÉ (1966) studied the floral nectary of *Ficaria*, and found that one of the most characteristic features of the ultrastructure is the presence of the membrane vesicles. He assumed that these vesicles of Golgi origin ensure the entry of the fluid into the nectarogenous cells by means of characteristic pinocytosis, move towards the plasmalemma, and secrete their content there. The observations of MERCER and RATHGEBER (1962) and FAHN and RACHMILEVITZ (1970, 1973) indicate that the nectar is secreted with the aid of the ER vesicles. In 1964, SCHNEPF assumed sugar transport by monomolecular means.

VASILIEV (1969) concluded from his studies that the protoplasm of the cells does not take part directly in the transport of the bulk of the nectar. He discounts the observations and conceptions of EYMÉ; the described high Golgi activity is valid only for the Ranunculaceae family, and the vesicles more distant from the Golgi cisternae are not of Golgi origin, but cross-sections of the ER. According to VASILIEV (1969), in the floral nectary of *Acer* the bulk of the phloem fluid bypasses the protoplasm of the cells and moves passively in the cell wall towards the secretion surface. A certain proportion of the quantity of nectar, however, does progress in the plasma of the secretory cells by means of active transport. And since the nectary cells absorb certain substances at the time of active secretion, from the fluid migrating along the cell wall, the protoplasm reabsorbs the necessary materials.

The presence of multivesicular bodies in the nectarogenous cells is mentioned by EYMÉ (1966), FINDLAY and MERCER (1971) and FAHN and RACHMILEVITZ (1970, 1973), who also point to their transport role.

In contrast with some of the above authors, we consider that the fluid transport is carried out by the lomasomes.

Very many authors have dealt with the lomasomes since the report of GILBART (1961), and their origin has been reviewed by MARCHANT and ROBARDS (1968). At

present their function has not been completely clarified: they may participate in the secretion, cell wall formation, haustorial absorption, glycogen synthesis, membrane proliferation, cytoplasm degeneration, response to stress, etc. (BRACKER, 1967; HUGHES and BISALPUTRA, 1970).

The phloem fluid, with a sugar content of 10—25%, passes the pores of the cribriform plate into the "transfusion" type cells, where the fluid is probably enclosed by cytoplasmatic membrane, and as lomasomes the phloem fluid containing vesicles traverse the plasmodesm to reach the adjacent glandular tissue cells.

These organelles, in relatively high numbers and forming a very large proportion of the amount of cytoplasm, appear in the glandular tissue cells. Their transport function is proved by Figs. 2—3.

The vesicles of the lomasomes contain the untransformed phloem fluid, in which the materials for reabsorption are also present. We assume that the fermentative transformation proceeds within this formation, whereby the mainly saccharose-containing fluid is converted to a sugary fluid with a composition charcteristic of the nectar of ricinus. The energy requirements of the process are provided by the mitochondria in reaction-proximity to the lomasomes (Fig. 2,2; Fig. 3, 1—2). The close connection of the ER and the lomasomes can similarly be observed (Fig. 3,3). Among the larger vesicles with a dense content, smaller vesicles, similar in size to the diameter of the ER and presumable of ER origin, are also present; these carry or transport the enzymes necessary for the carbohydrate metabolism to the site of reaction.

The lomasomes can not have a cell wall accumulating effect, since in the period of secretion (ca. 10 days) no substantial wall-forming processes take place. Moreover, for a possible minimal cell-wall accumulating process neither is it considered necessary for the lomasomes to take part with such an appreciable volume, and to migrate in those cells in which the main function in the given period is the fermentative transformation and the transport.

The presence of lomasomes was not observed in cells not carrying out secretion. The appearance of the peroxysomes is striking; this indicates that the function of the nectarogenous cells is changed. The lamellar system of the chloroplasts is developed (Fig. 4,3) and the gland now acquires the bulk of the carbohydrates required for the vital processes of the cell in the course of photoreactions.

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ULTRASTRUCTURAL STUDIES ON AMENTIFLORAE POLLEN GRAINS, II

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Abstract

This paper is the second part of our TEM investigations on Amentiflorae taxons. The genera *Carpinus, Ostrya, Zelkova, Ulmus, Humulus, Morus* and *Urtica* were investigated. It is concluded that some of the fine structural features in the Amentiflorae taxons are of general, while others of special character. The ultrastructural features can be used for elucidation the question of relationship between different genera.

Introduction

In a previous paper (KEDVES and PÁRDUTZ, 1973) we touched briefly on the necessity of ultrastructural studies on the exines of Amentiflorae taxons. Our results on the exine ultrastructure of some Brevaxones pollen grains were reported earlier. These studies have been continued in accordance with the points of view put forward. The material in the present examinations extended to *Carpinus, Ostrya, Zelkova, Ulmus, Humulus, Morus* and *Urtica* genera. The method was the same as described previously.

Results

Carpinus **L.** Fig. 1.

Examinations were made on *Carpinus betulus* **L.** and *C. duinensis* SCOP. No essential ultrastructural difference was observed between the two species. Extragerminal exine. — Tectate, perforated with narrow channels. The surface of the tectum is uneven, and sparsely ornamented with spinae. The elements of the columellae are of various shapes: spherical, ellipsoid and columnar, and are mostly situated in one, or rarely two rows. The foot layer is very thin, and it did not prove possible to observe a marked endexine under it on our ultrathin sections. T/C/F (ratios of the thicknesses of the tectum, the columellae and the foot layer)= =3—4/2—3/1 (Fig. 1,1). Pore wall exine (Fig. 1,2—4). The tectum is attenuated in the vicinity of the pores, inclines in the centripetal direction, and breaks around the middle of the annulus. The elements of the columellae accumulate strongly, generally comprise 7—8 rows and form the annulus. The foot layer breaks at the level of the beginning of the annulus, and thus an atrium is formed. Before the atrium, below the foot layer, an endexine of pronounced lamellar ultrastructure appears, and this by and large runs intermittently through below the annulus.

Ostrya SCOP. (Fig. 2)

Examinations were made on *Ostrya carpinifolia* SCOP.

Extragerminal exine. — Tectate, perforated with extremely narrow channels. There are large, wide-based spinae on the surface of the tectum. The elements of the columellae are generally spherical, and arranged in 1—2 rows. The foot layer is narrow. T/C/F=3—4/1,5/1. (Fig. 2,1).

Pore wall exine. — The tectum inclines in the centripetal direction along the pores, attenuates and breaks. The elements of the columellae accumulate only slightly in the pore wall region and form the annulus. The columellae here are generally 4-rowed. The foot layer breacks around the base of the annulus, and thus in essence an atrium is formed. No endexine was observed in the pore wall region either.

Zelkova SPACH (Fig. 3)

Examinations were made on *Zelkova cretica* SPACH.

Extragerminal exine. — The tectum is perforated with relatively narrow, frequently difficulty observable channels. The surface is uneven, and ornamented sparsely with small spinae. The columellae below the tectum consists of spherical or ellipsoid anastomizing elements, the latter being very small and arranged in 10—16 rows. Before the foot layer the elements of the columellae are larger and sparsely arranged. They are 2—3 times as large as the previous ones, and similarly spherical (Fig. 3,2—5). The foot layer is narrower at the tectum too, and below it there is sporadically endexine of narrow granular ultrastructure. T/C/F= =1.5/10—15/1.

Pore wall exine. — In the pore wall region the endexine of granular ultrastructure is pronounced. The foot layer similarly breaks before the pores, but the endexine takes over its place, and thus the atrium forms an interesting case. Before the pores, in the vicinity of the pore-channel, it is mainly spherical, and there is a formation corresponding to the foot layer. The tectum inclines at the pores. The elements of the columellae are strongly accumulated and form the annulus.

Ulmus L. (Fig. 4)

Examinations were made on *Ulmus americana* WILLD. and *Ulmus japonica* SARG.

Extragerminal exine. — Tectate, perforated with narrow channels, and the surface of the tectum is ornamented with small spinae. The surface is strongly undulated, a consequence of the light-microscopially known sculptura. The foot layer is extremely narrow. For the columellae essentially the same could be established as with the examined species of the *Zelkova* genus; as regards its size the columellae above the foot layer differs from the other parts of this layer. The columellae are arranged in 6—15 rows. T/C/F=1.5/10—20/1. (Fig. 4,1—3).

Pore wall exine. — The tectum inclines centripetally along the pores, and then breaks. The elements of the columellae accumulate and form the annulus. The foot layer breaks at the level of the pore, and thus we can speak of an atrium. Endexine could not be observed with certainty even in the pore wall region (Fig. 4,4).

Humulus L. (Fig. 5)

Examinations were made on *Humulus japonicus* SIEB. and ZUCC.

Extragerminal exine. — Tectate, perforated sparsely with narrow channels; the surface is ornamented with wide-based large spinae. The elements of the columellae are of various shapes: spherical, ellipsoid and columnar, they frequently anastomize, and are arranged in 1—2 rows. Compared to the previous two layers the foot layer is extremely thin. T/C/F=6—8/4—5/1.

Pore wall exine. — The tectum inclines along the pores and generally breaks at the level of the foot layer without attenuation. The elements of the columellae accumulate strongly and form the annulus, but there is an appreciable drop-shaped cavity below the thickening columellae. The foot layer generally breaks at the base of the annulus and its place is assumed by endexine with difficulty distinguishable granular ultrastructure (Fig. 5,1). At times the breaking of the foot layer can not be observed with certainty, and the endexine is difficult to distinguish from the foot layer.

Morus L. (Fig. 6)

Examinations were made on *Morus nigra* L. and *Morus indica* L. In this case noteworthy differences were observed in the pore wall regions of the two species.

Extragerminal exine. — Tectate, perforated with narrow channels. There are wide-based large spinae on the surface of the tectum. The elements of the columellae are arranged in 2—3 rows, and are small and generally spherical. In this genus too the foot layer is very narrow compared to the other layers. T/C/F= =5—6/3/1. (Fig. 6,1).

Pore wall exine. — In *Morus nigra* there is an endexine of extremely developed, lamellar ultrastructure in the pore wall region. The tectum and the columellae are unchanged in the pore wall region, and break at the level of the pores. The foot layer breaks at the base of the thickening endexine, and thus there is an atrium, but without an annulus of ectexine origin. The elements of the endexine form a developed endannulus. In *Morus indica* the difference primarily lies in the fact that part of the pore wall endexine carries an "operculum" in the pore, and part of the ectexine, the tectum and the columellae, a small part of it, probably spherical in shape. The endannulus is not so pronounced as in the former species (Fig. 6,4).

Urtica L. (Fig. 7)

Examinations were made on *Urtica diodica* L. Its pores are arranged strongly subequatorially, and thus there was no means of studying the entire ultrastructure of the pore wall region. The extragerminal exine is tectate and not perforated, the surface of the tectum is undulated, and on it there are blunt or sharp-ended ornamental elements. The elements of the columellae are spherical, and generally arranged in 2 rows. T/C/F=2—3/2/1. In the pore wall region the foot layer breaks (Fig. 7,1—2), and the elements of the columellae accumulate a little.

Discussion

Comparison of the present data with the earlier results leads to the following conclusions: The new data too show the channels in the tectum to be extremely widespread; only in the *Cannabis* and *Urtica* genera did they not appear. Spinae

occurred without exception in the Amentiflorae species previously examined. Two types can be distinguished here; the extremely narrow-based, relatively short *Carpinus, Ostrya, Zelkova* and *Ulmus,* and the relatively large and wide-based *Humulus, Morus* and *Urtica.* The columellae are very characteristic in the *Zelkova* and *Ulmus* genera, in that the ultrastructural elements in the part directly above the foot layer are larger than in the part above this. In spite of the fact that it proved possible to detect endexine in *Zelkova cretica,* which is not known for the hitherto examined pollen exines of the Juglandaceae, the exine ultrastructures of the *Ulmus* and *Zelkova* genera resemble those of the Juglandaceae *Carya* and *Juglans* genera, but definitely differ from the other Amentiflorae in their characteristic columellae. Also similar to one another are the columellae of the *Carpinus* and *Humulus,* and the *Ostrya* and *Morus* genera.

Endexine of granular ultrastructure can also appear independently of the other features of the ectexine, e.g. in *Zelkova cretica, Humulus japonicus* and the previously studied *Cannabis sativa.* A developed lamellar endexine occurred in the *Morus* genus, and is also known in the pore wall region of Corylaceae and Betulaceae. The development of the endannulus is similarly characteristic in the *Morus* pollen grains by way of the strong accumulation of the endexine lamellae.

Our new data have confirmed that the annulus is formed in the Brevaxones pollen grains by the accumulation of the elements of the columellae, and with the exception of the *Morus* genus occurred in every species examined. A difference can be observed in *Humulus japonicus,* where there is a consequential cavity between the pore wall columellae and the endexine. Pores appeared in the *Zelkova, Ulmus* and *Humulus* genera, and from this respect too this latter genus differs from the type regarded as general, for the foot layer breaks in the pore wall region and its place is taken over by the endexine. In contrast with the earlier data, of interest is the operculum of ectexine origin above the pores of *Morus indica.* The atrium in the *Carpinus* and *Ostrya* genera is a new ultrastructural addition as regards the pore wall exine of *Myrica* type, since the exact demonstration of this on the basis of light-microscopic examinations is fairly problematical.

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Fig. 1. *Carpinus duinensis* SCOP.

1. — Ultrastructure of the extragerminal exine. M: x25 000.
2. — Ultrastructure of the pore wall exine. M: x25 000.
3. — Exine ultrastructure in the vicinity of the pore well region. M: x25 000.
4. — Tectum and columellae in the vicinity of the pore wall region. M: x25 000.
sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer, En=endexine.

Fig. 2. *Ostrya carpinifolia* SCOP.

1. — Ultrastructure of the pore wall exine. M: x25 000.
2. — Ultrastructure of the extragerminal exine. M: x50 000.
sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer.

Fig. 3. *Zelkova cretica* SPACH.

1. — Ultrastructure of the pore wall exine in the vicinity of the pore wall region. M: x25 000.
2—5. — Details from the ultrastructure of the extragerminal region. M: x25 000.
sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer.

Fig. 4. *Ulmus americana* WILLD.

1—3. — Ultrastructure of the extragerminal exine. M: x25 000.
Ulmus japonica SARG.
4. — Ultrastructure of the pore wall region. M: x25 000.
sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer.

Fig. 5. *Humulus japonicus* SIEB. and ZUCC.

1. — Ultrastructure of the pore wall region. M: x50 000.
2. — Outline picture of the ultrastructure of the pore wall and extragerminal exines. M: x25 000.
sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer, En=endexine.

Fig. 6. *Morus nigra* L.

1. — Ultrastructure of the extragerminal exine. M: x50 000.
2. — Ultrastructure of the pore wall region in the vicinity of the pore wall region. M: x25 000.
3. — Ultrastructure of the pore wall region in the pore wall region. M: x25 000.
Morus indica L.
4. — Ultrastructure of the pore wall region in the pore wall region. M: x25 000.
sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer.

Fig. 7. *Urtica dioica* L.

3,2. — Exine ultrastructure in the vicinity of the pore wall region. M: x50 000.
1,4. — Ultrastructure of the extragerminal exine. M: x50 000.

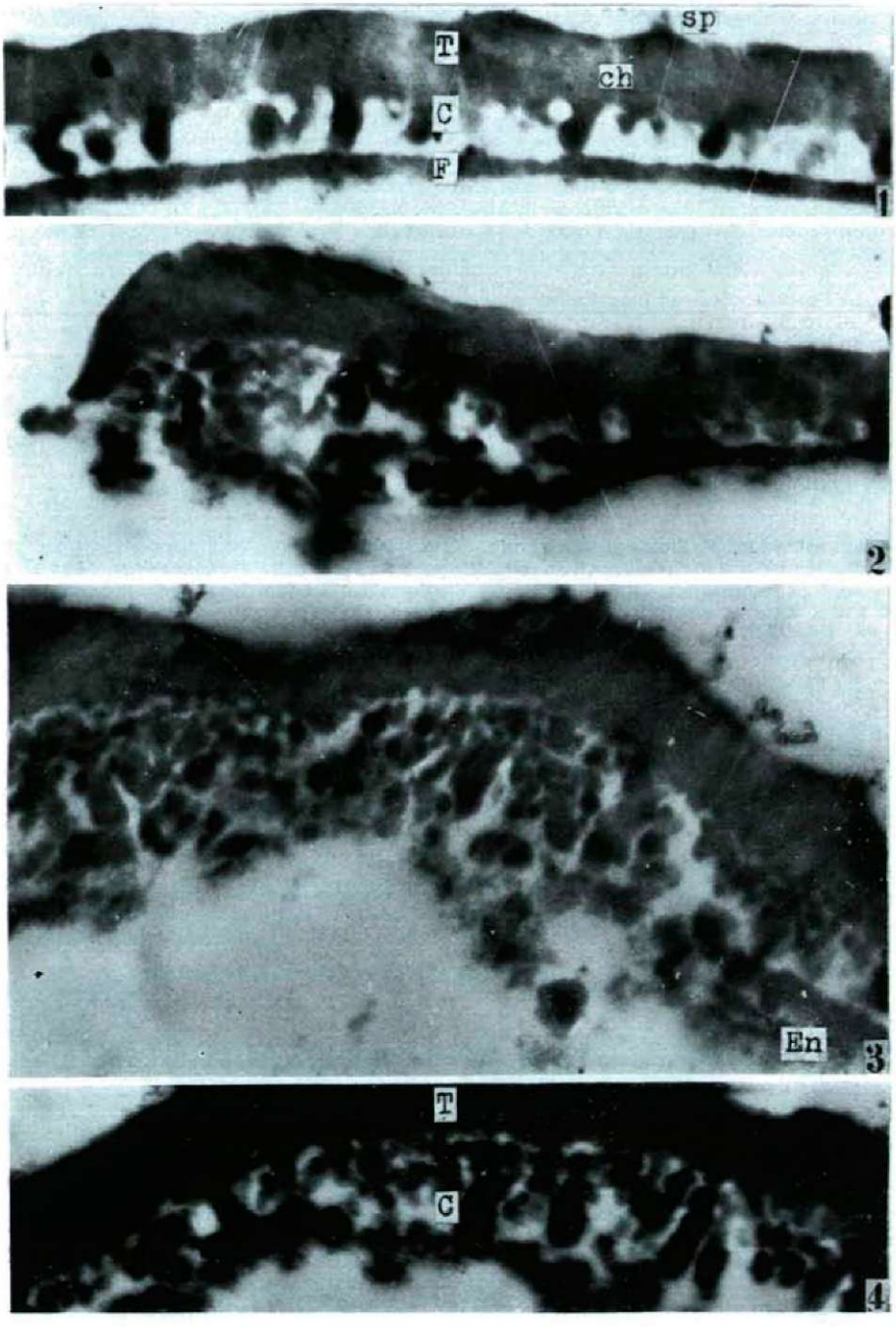
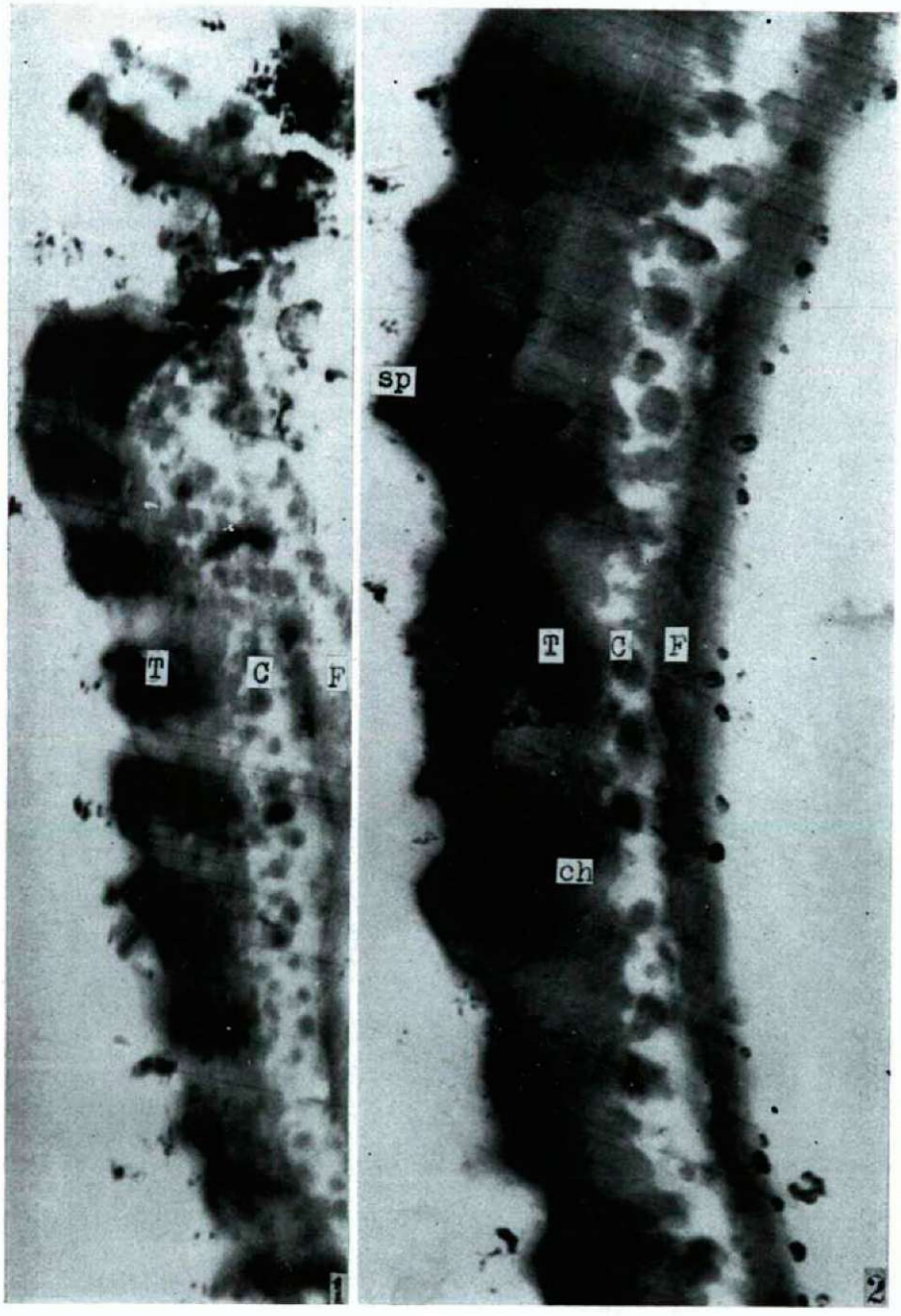


Fig. 1



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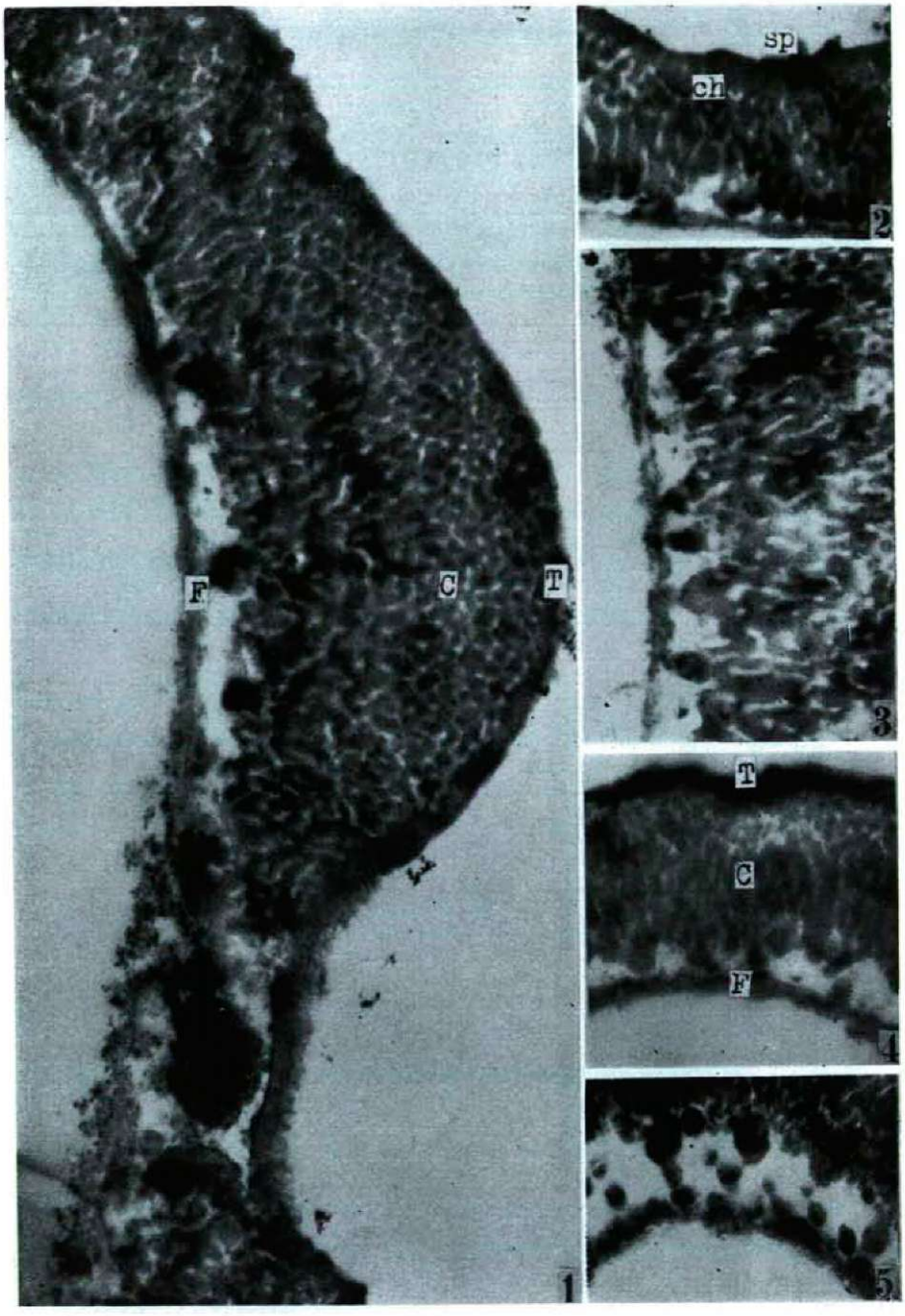

Fig. 3

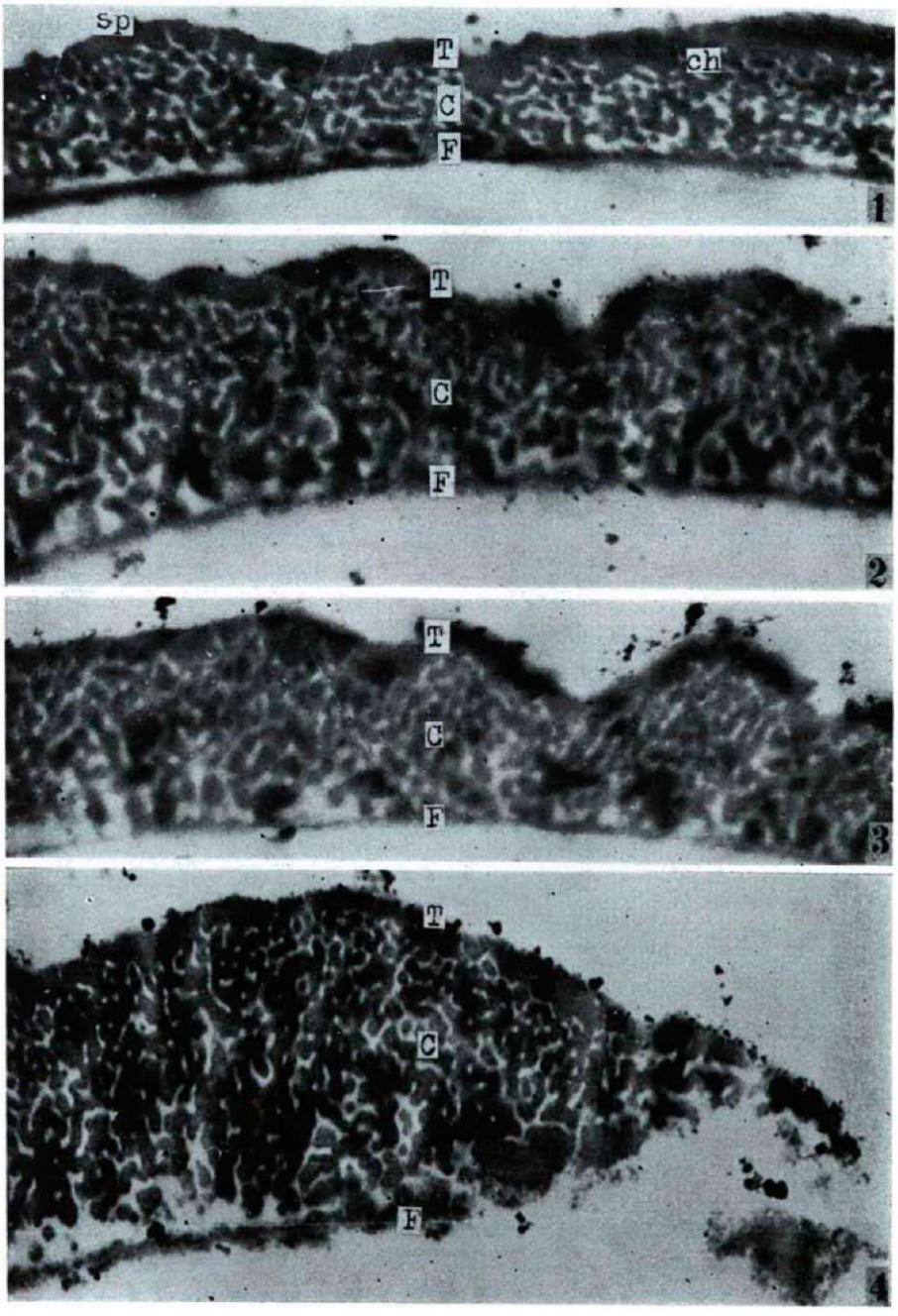

Fig. 4

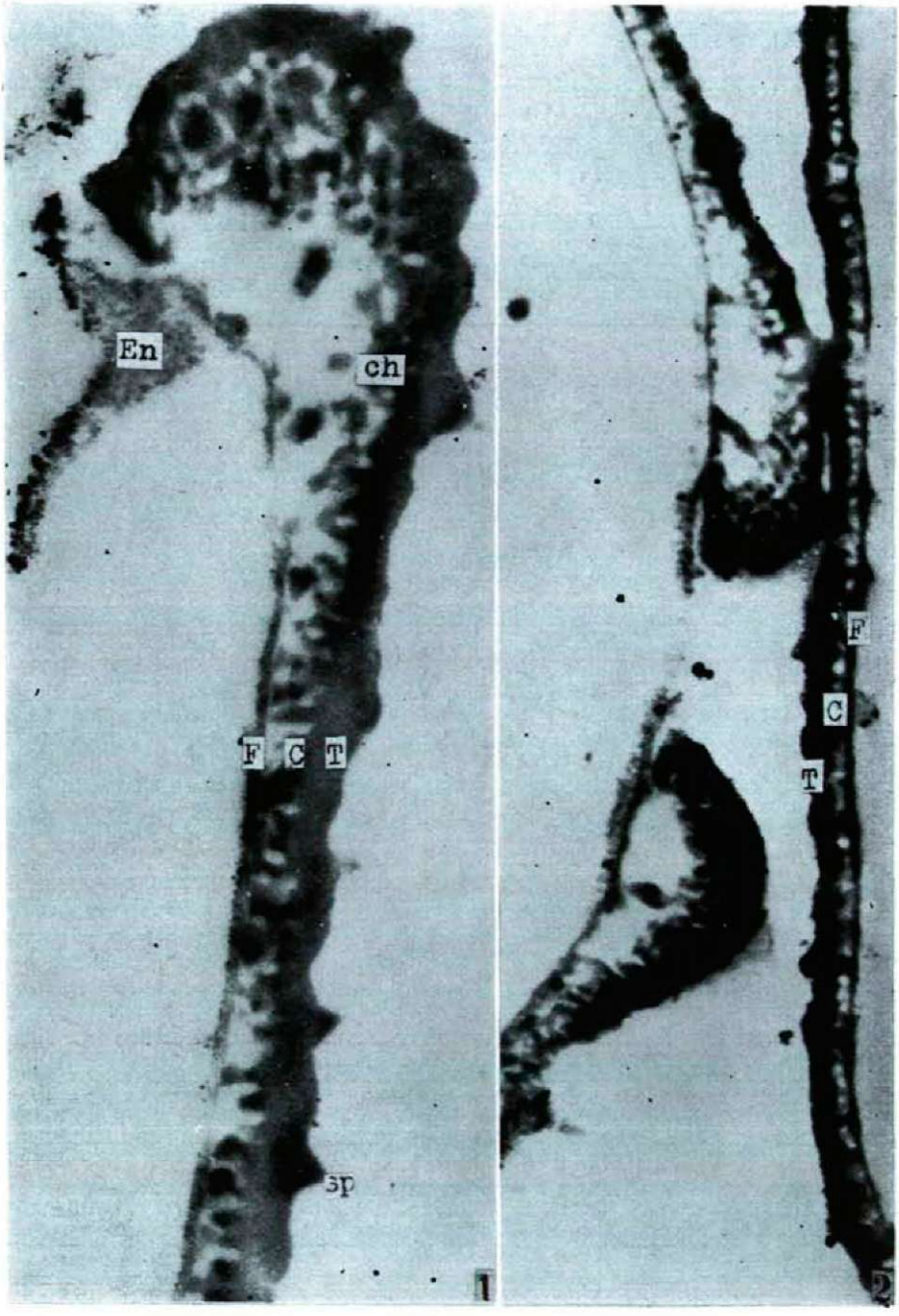

Fig. 5

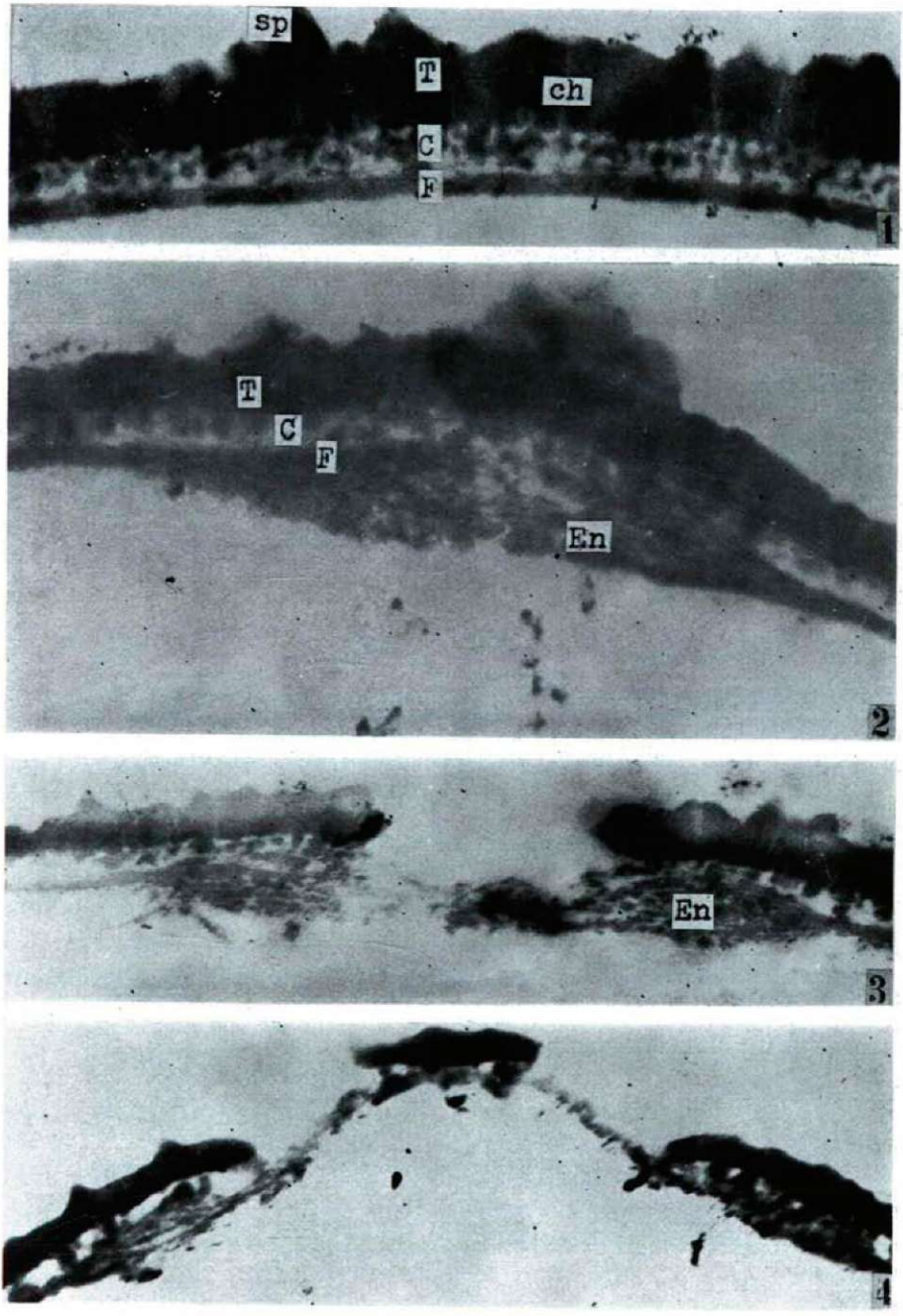

Fig. 6

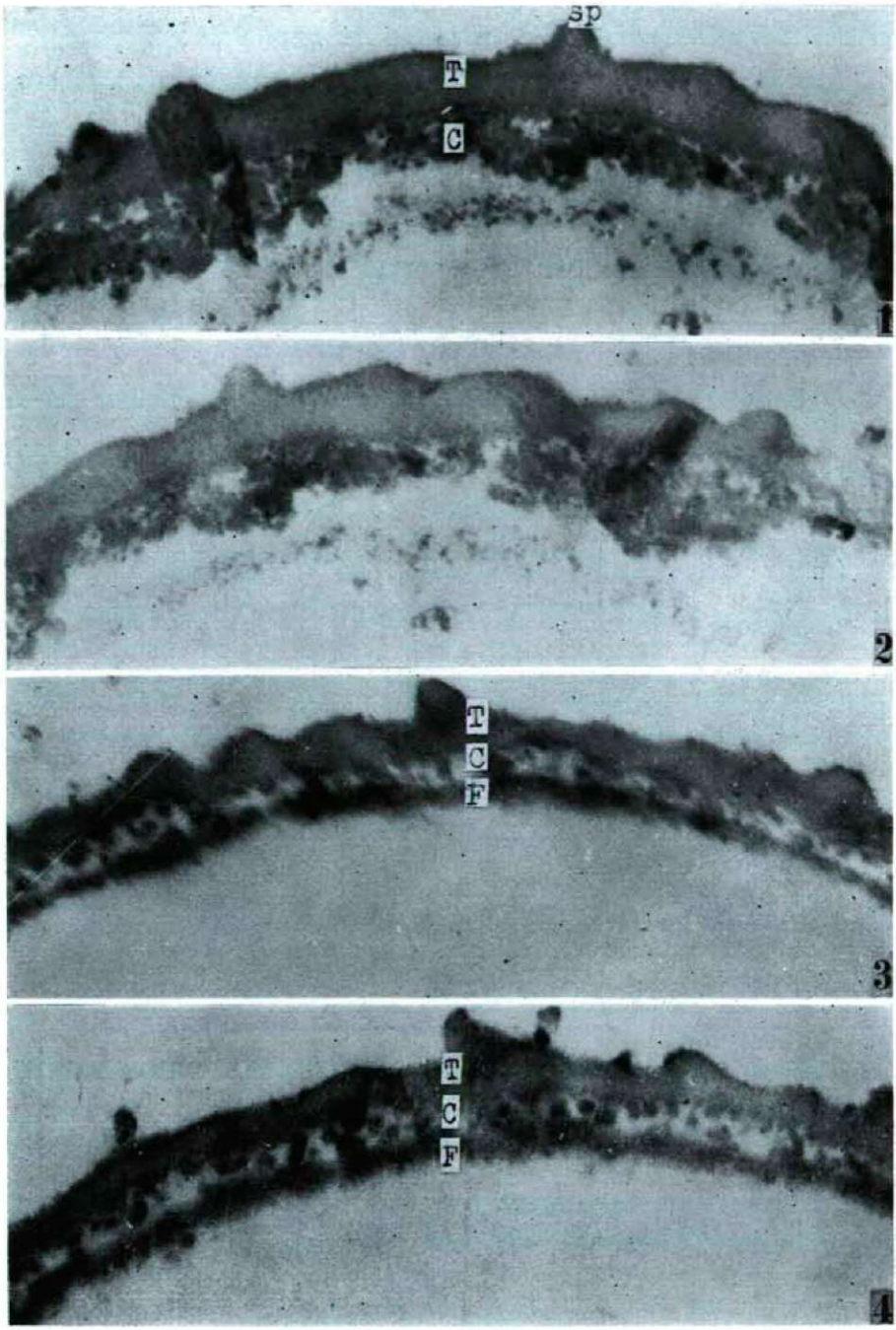

Fig. 7

Acta Biologica Szeged. *20* (1—4), pp. 81—88 (1974)

ULTRASTRUCTURAL STUDIES ON MESOZOIC INAPERTURATE GYMNOSPERMATOPHYTA POLLEN GRAINS

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Abstract

Fine structural investigations were performed on Gymnospermatophyta pollen grains from the Nubian formation of the Oasis Farafra. The fine structure of *Inaperturopollenites limbatus* exine (lower level of Nubian formation; Jura era) corresponds in general to the wall of the palaeozoic Schopfipollenites species. The *Araucariacites* species from the upper level (Upper Cretaceous) however, are identical from ultrastructural point of view with the recent Gymnospermatophyta exines.

Introduction

The basis of the knowledge of the Mesozoic Gymnospermatophyta exine ultrastructure was established by PETTITT and CHALONER (1964) with their ultrastructural studies of the exines of *Classopollis*-type pollen grains. PETTITT (1966) reported very valuable data on the submicroscopic structures of Palaeozoic spores and primitive Gymnospermatophyta pollen grains. In studies on Jurassic and Upper Cretaceous Gymnospermatophyta exines, KEDVES and PÁRDUTZ (1973) obtained results suggesting the necessity to broaden the previous investigations. Thus, the exine ultrastructure of the Jurassic *Spheripollenites scabratus* COUPER 1958 agrees markedly with those of Angiospermatophyta ectexines, while the cf. *Araucariacites* v. *Granulatisporites* fsp. is of an angiospermid character. This justified the ultrastructural examination of other inaperturate pollen grains, and the present paper gives our recent results in this respect.

Materials and Methods

From the point of view of the aim of the examination, samples from the Nubian formation of the Farafra oasis, already studied with regard to their main light-microscopic types, were the most suitable. As reported previously (KEDVES, 1971), the lower level of the formation is Jurassic, and its upper level Upper Cretacean. The Jurassic samples contained great numbers not only of the *Classopollis* genus, but also of *Inaperturopollenites limbatus* BALME 1957, while in the Upper Cretacean samples pollen grains of the Araucariacites form-genus were comparatively frequent. The preparation of the examination material and the method used were described earlier (KEDVES and PÁRDUTZ, 1970).

Results

1. *Inaperturopollenites limbatus* BALME 1957 (Fig. 1, 2).

Note. — This differs substantially from the other, particularly Lower Tertiary inaperturate pollen grains; the exine attenuates strongly at its poles, and the wall is thicker along the "equator".

Examinations were made on five specimens, and the exine ultrastructure of the pollen grain could be regarded as completely elucidated. The exine is of a markedly gymnospermid character, and consists of ectexine and lamellar endexine, while the ectexine is not triply divided. In many cases the lamellar ultrastructure of the endexine is not pronounced; this is probably a result of secondary change following fossilization. In the equatorial part the ectexine is 2—3 times thicker than the endexine; it has a "sponge structure" and consists of anastomizing elements of variable form (Fig. 1,4; Fig. 2). The ultrastructural elements are arranged a little more densely in the vicinity of the surface than in the inner parts, at times giving the impression of a separate layer. The endexine has a markedly lamellar ultrastructure (Fig. 1,2,4). In the polar, attenuating part the thickness of the ectexine is by and large the same as that of the endexine. As regards its essence, the ultrastructure of the ectexine in this part agrees with that of the equatorial part, with the difference that its elements are arranged a little more densely (Fig. 1,3).

2. *Araucariacites* fsp.$_1$ (Fig. 3)

In this form-species too the exine is distinctly divided into two layers, ectexine and very finely lamellar endexine. The ectexine consists of elements of variable form: drop-shape, spherical or ellipsoid. As regards its size, two types can be established. The smaller ones, which are primarily spherical or ellipsoid in shape, are situated immediately above the endexine. Among these can be found the larger, drop-like or radially extended elements, which are frequently ramified at their terminals, with pointed or blunt-ended processes.

3. *Araucariacites* fsp.$_2$ (Fig. 4)

As regards its fundamental ultrastructural features, this is the same as the previous form-species. A difference can be established in the ectexine: in this pollen grain the relatively large ultrastructural elements are approximately spherical or ellipsoid in form, without tapering processes. The smaller ectexine elements frequently anastomize.

Discussion

Comparison of these more recent results with the earlier findings leads to the following conclusions. The submicroscopic structure of the walls of the Palaeozoic Gymnospermatophyta micro-residues examined from several aspects by PETTITT (1966) is heterogeneous. Main types:

1. Completely homogeneous wall-structure; *Didymosporites scotti* CHALONER.
2. The outer layer is fibrillar, and the inner layer homogeneous; *Cystosporites giganteus* (ZERNDT) SCHOPF 1938.
3. The wall consists of uniformly three-dimensional sporopollenin elements which form a spongy structure; *Trigonocarpus* sp.

4. The outer layer is a spongy layer, and the inner layer has granular ultrastructure; *Florinites* sp.

5. The outer layer is spongy, and the inner lamellar; *Schopfipollenites* sp. This ultrastructure agrees with that of *Inaperturopollenites limbatus* BALME 1957. As regards ultrastructure, therefore, this Jurassic "inaperturate" pollen grain represents a very primitive type. From this point of view, of particular interest is the earlier studied *Spheripollenites scabratus* COUPER 1958, the exine of which consists only of ectexine, and this is of triple "angiospermid" division (tectum, columellae, foot layer). The ultrastructure of pollen grains of the *Classopollis* type (PETTITT and CHALONER 1964) is even more complex than that of the Angiospermatophyta. Thus, in the Jurassic the angiospermid too occurs in addition of the primitive exine ultrastructure in the inaperturate pollen grains. The Upper *Cretacean* cf. *Araucariacites* v. *Granulatisporites* fsp. (KEDVES and PÁRDUTZ, 1973) similarly has an ultrastructure reminiscent of the Angiospermatophyta. The significance of the exine ultrastructure of *Araucariacites* fsp.$_{1\ 2}$, also originating from this age, lies in the fact that this is the first successful demonstration of an ultrastructure of Gymnospermatophyta type similar to recent taxons in fossil inaperturate pollen grains. The data referring to the recent taxons can be found in the papers of GULLVAG (1966) and PETTITT (1966).

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Fig. 1. *Inaperturopollenites limbatus* BALME 1957

1. — Light-microscopic picture of ultrastructually studied specimen in embedded material. M: x1000
2. — Ultrastructure of the endexine. M: x25 000.
3. — Ultrastructure of the exine on the polar, attenuating wall-part. M: x25 000.
4. — Ultrastructure of the exine on the equatorial thicker wall-part. M: x25 000.
   Ectex.=ectexine, Endex.=endexine.

Fig. 2. *Inaperturopollenites limbatus* BALME 1957

1. — Partial tangential section of the ectexine. M: x25 000.
   Ectex.=ectexine, Endex.=endexine.

Fig. 3. *Araucariacites* fsp.$_1$

1. — Light-microscopic picture of ultrastructurally studied specimen in embedded material.
2. — Tangential section of the ectexine. M: x25 000.
3,4. — Cross-section of the exine. M: x25 000.
   Ectex.=ectexine, Endex.=endexine.

Fig. 4. *Araucariacites* fsp.$_2$

1. — Light-microscopic picture of ultrastructurally studied specimen in embedded material. M: x1000.
2. — Cross-sectional picture of the exine. M: x50 000.
3. — Tangential section of the ectexine, from the part above the endexine. M: x25 000.
4. — Tangential section of the ectexine, from the level of the larger ultrastructural elements. M: x25 000.
5. — Cross-sectional picture of the exine. M: x50 000.
   Ectex.=ectexine, Endex.=endexine.

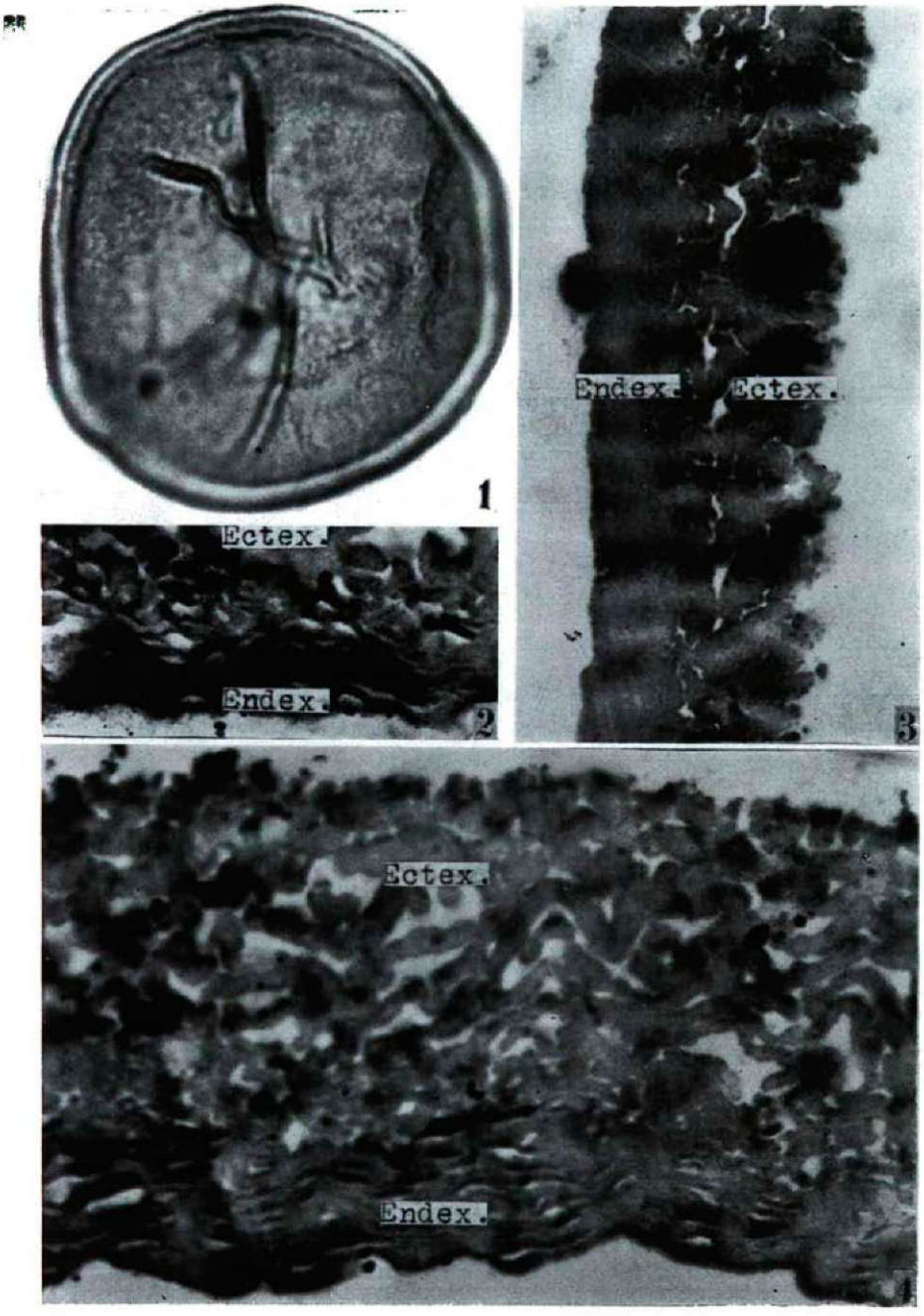

Fig. 1

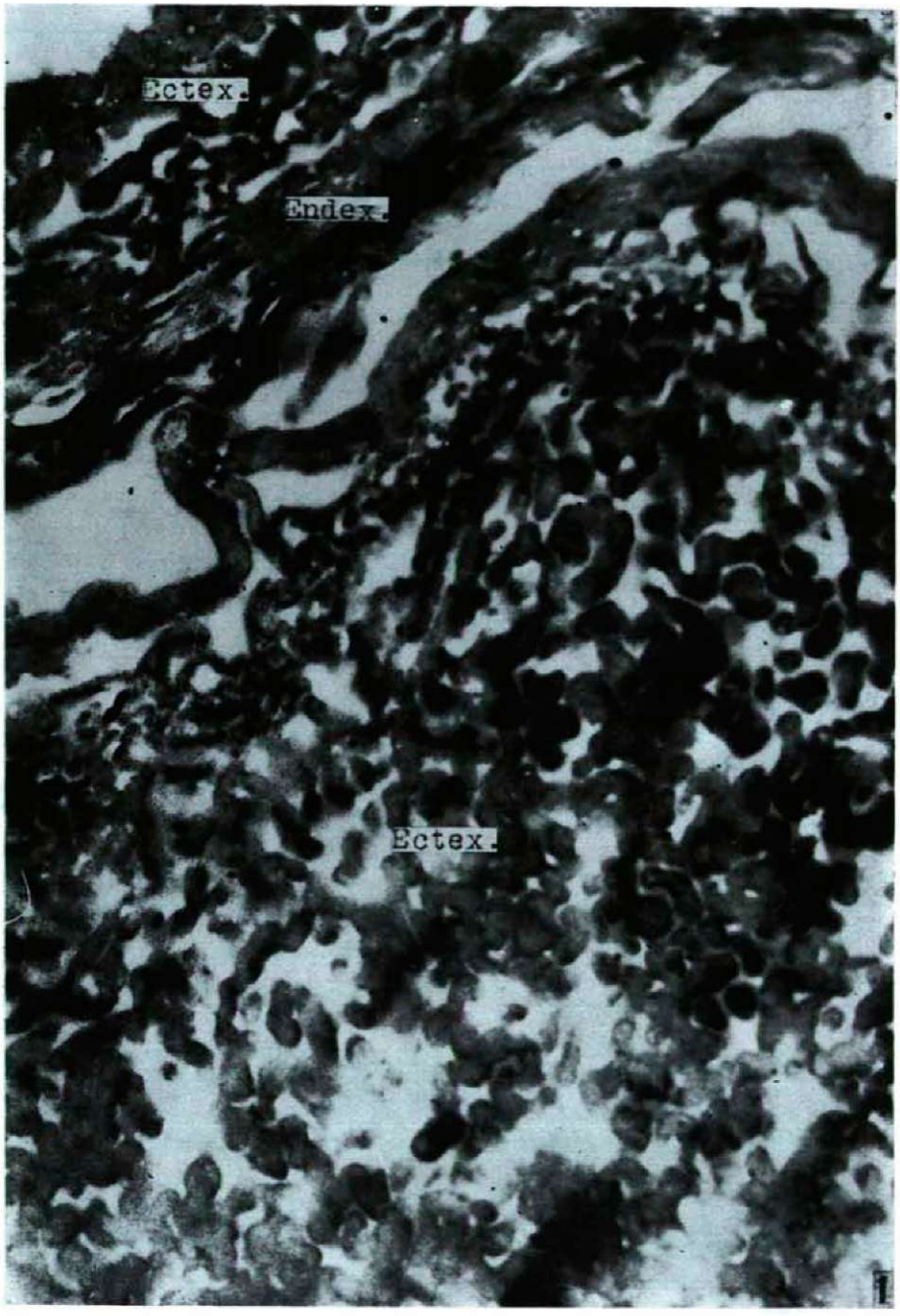

Fig. 2

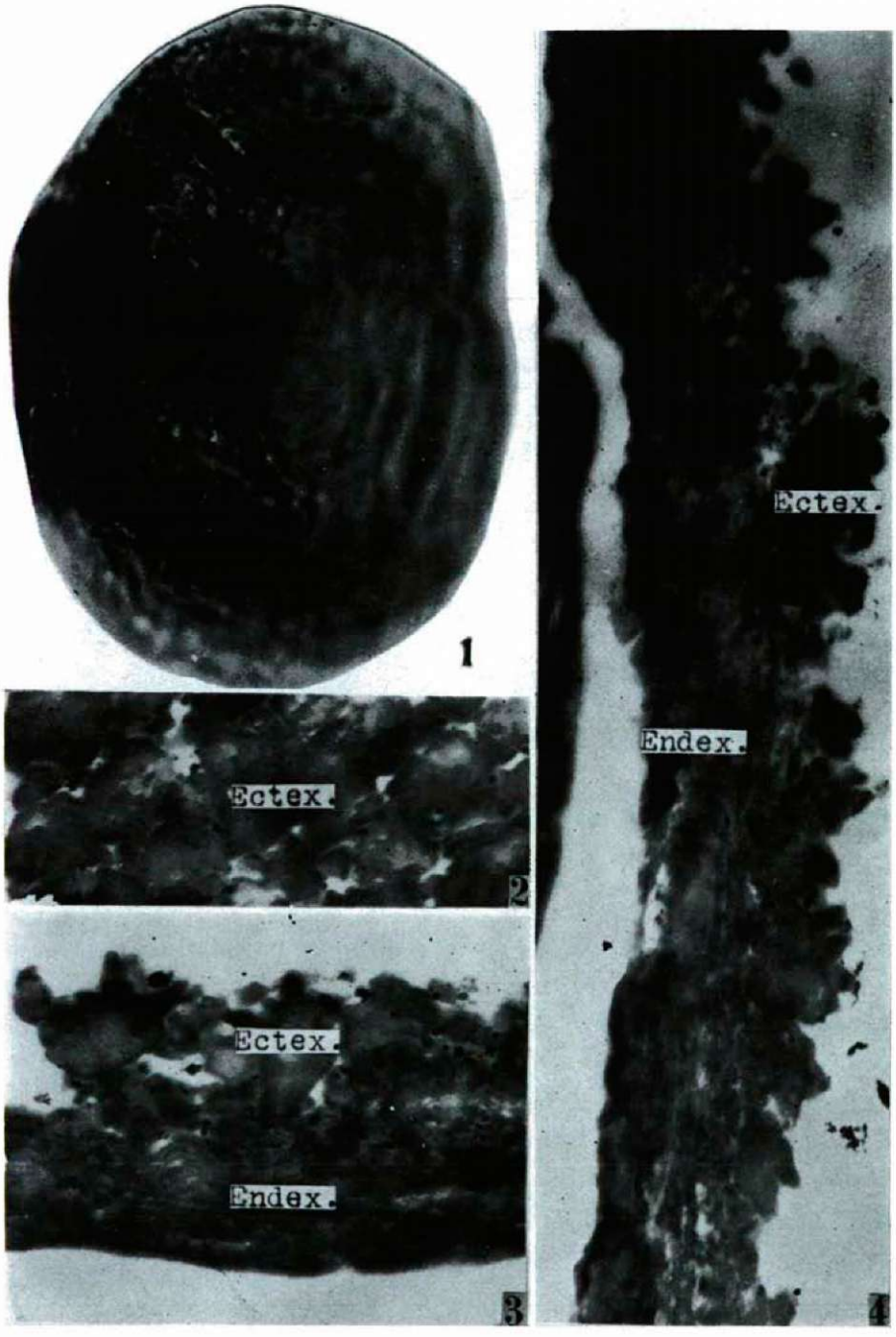

Fig. 3

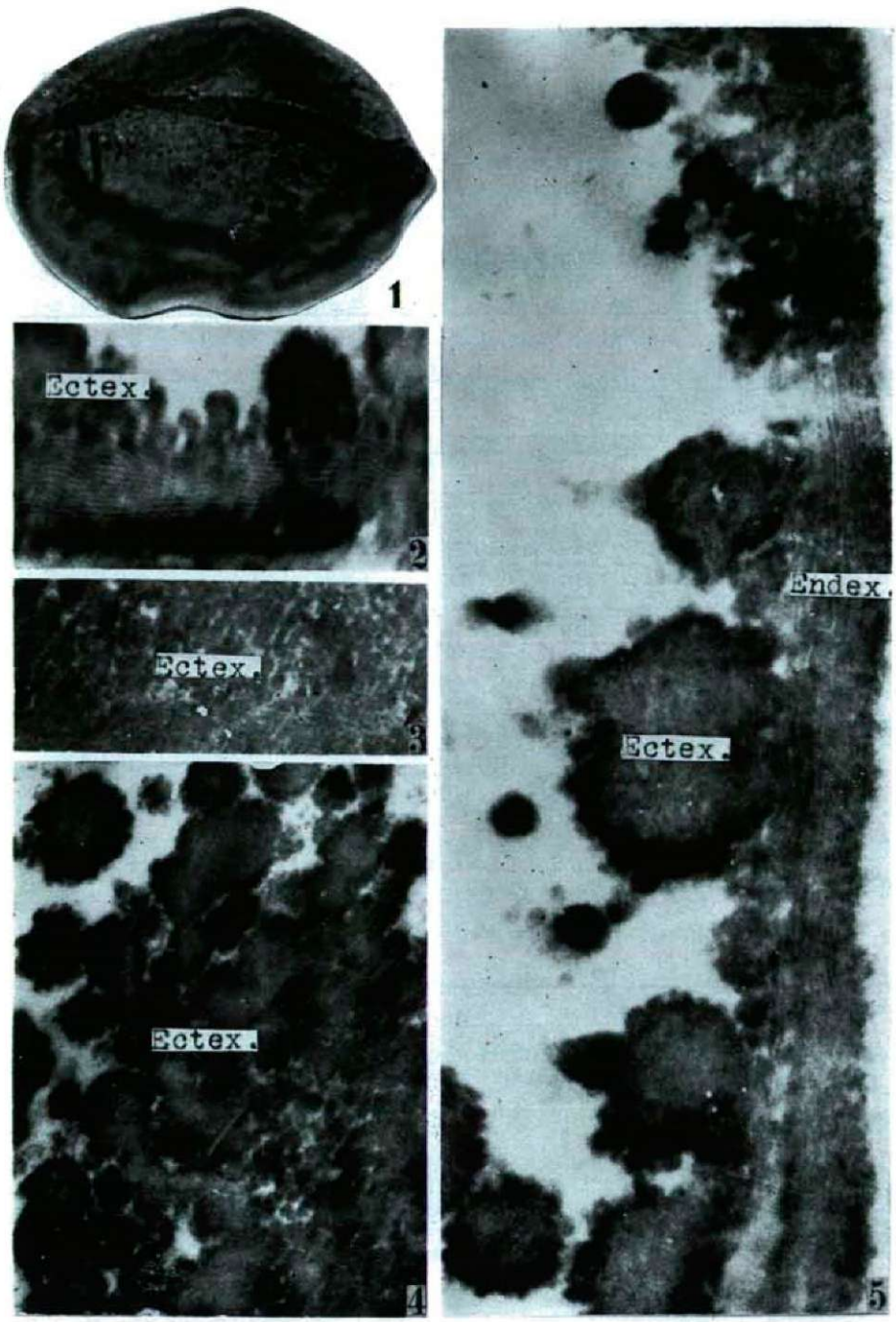

Fig. 4

Acta Biologica Szeged. *20* (1—4), pp. 89—93 (1974)

SENSITIVITY TO LIGHT IN PLANTAGE SEEDS AS RELATED TO SEED COAT STRUCTURE

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(Received July 21, 1973)

Abstract

The seeds of three different species of *Plantage*, namely *P. crassifolia, P. major* and *P. squarrosa*, were studied with regard to their varying sensitivities to light.

It was found that the seeds of *P. major* were the smallest in size among the three species studied and exhibited the highest degree of sensitivity to light during germination, being light-favoured. *Plantage crassifolia* and *P. squarrosa* had larger seeds and showed lesser sensitivities to light during germination.

The cause of such differences was sought in the seed coat structures of the different species. The seeds of Plantage major contained a well-defined, pigment-full cellular palisade layer, which is not present in the other two species.

Phylogenetic relations among the three species under investigation were discussed in the light of their behaviour during germination.

Introduction

In a previous investigation (TADROS and REZK, 1966), it was shown that the seeds of some species of Plantago exhibit varying degrees of sensitivity to light during germination. Thus, in complete darkness, the seeds of the species studied showed low germination percentages, that differed from one species to another. The results of the above-mentioned investigation showed that the seeds of *Plantago major* gave 2% germination in the dark, and 66% in bright daylight: those of *P. crassifolia* gave 12% and 38% respectively, in the two treatments; while those of *P. squarrosa* gave 50% and 92%.

Further work (REZK 1967a, 1967b; REZK et HORVÁTH, 1968) was carried out with the seeds of *P. major*, in which the phenomenon was studied from the points of view of the effects of different chemical and physical factors on the breaking of the dark-induced dormancy. It was concluded that the behaviour of *P. major* seeds differed considerably from that of *Lactuca sativa* v. Grand Rapids, experimented on in similar investigations by many other authors (e.g. BORTHWICK et al., 1954).

For *Plantago major* seeds it was observed in common practice in our laboratory that scratching them with sand paper resulted in a rapid onset and a high percentage of germination in the absence of the brinht daylight usually needed. This has drawn attention towards a possible role of the seed coat in previnting the seeds from germination in the dark. Seed coat dormancy in general is a wellknown phenomenon previously investigated by CROCKER et BARTON (1953) and others.

The aim of the present investigation is to answer the questions: a) Is there any probable correlation between the varied sensitivities to light in the seeds of the species of *Plantago* studied and their morphological structures. b) Can this variation in sensitivity to light be correlated the their previously suggested interspecific phylogenetic relationships (TADROS et REZK, 1970).

Materials and Methods

Seeds of *Plantage crassifolia* FORSK., *P. major* L. and *P. squarrosa* MURR. v. *brachystachys* BOISS. were collected from naturally-occurring plants in the vicinity of Alexandria. Microtome sections (20 μ thick) were prepared, which were stained with crystal violet (saffranin. Free-hand sections mounted in water were also prepared for comparison, as the colouring material was not leached out in the latter.

Observations

The seeds of the three species showed considerable morphological variation. *Plantago crassifolia* and *P. squarrosa* seeds are lightbrown in colour with a smooth testa, while those of *P. major* darker sculptured testa. Further, the general shape of the seed differs from one species to another. *P. squarrosa* seed is nearly ellipsoidal in outline and concave-convex in T. S. measuring about 1.5—2 mm long. *P. Crassifolia* seed is narrower and more or less plano-convex in T. S. reaching 1.0—1.5 mm in length. *Plantago major* seed is triquetrous to irregular in outline, and nearly triangular in T. S.; it measures about 1 mm long.

Examination of the median transverse sections of the seeds of the three species of *Plantago* reveals basic differences both in shape and in the structure of the testa. They all agree in possessing a thin, delicate, mucilageproducing epidermal layer. This layer has previously been studied in considerable detail for two species of *Plantago*. DODDS (1953) described it in *P. coronopus* seed from the point of view of its ecological value to the plant as a cementing material, that fixed the seed in the soil and allows the growing radicle to penetrate it easily. With regard to the development HYDE (1970) examined and described a similar layer in the related species *Plantago ovata*.

Below the epidermis in *Plantago squarrosa* and in *Plantago crassifolia* there is a layer of undifferentiated compact cells that contain a brown colouring material, responsible for the seed colour. This is the pigment layer. In the former species this layer becomes thinner on the hylar side of the seed.

In *Plantago major* on the other hand, below the transparent epidermis lies a definite layer of cells whose radial and inner tangential walls are densely thickened and pigmented. This is the palisade or the malpighian layer. It is to this layer that the dark colour of the testa and its sculptured appearance are due. This colouring material seems to be lost during dehydration and staining techniques, so that the thickened walls are colourless in the permanent microtome sections. In the free-hand section mounted in water, it retains the colour and shows a definite dark-coloured cellular layer. The thickening is shown to be deposited in the from of radial striations. This palisade layer tightly ensheathes the contents of the seed below the epidermis.

Similar testa structures in the seeds of some crucifers have been reported by EDWARDS (1968), and VAUGHAN (1956 and 1970). This is especially met with in *Brassica* spp. and *Sinapis* spp., which are reported to exhibit some type of dormancy.

Discussion and Conclusions

It is clear from the above study that there are basic differences in the structures of the three species of *Plantago* studied, parallel to their degrees of sensitivity to light. As the pigmentcarrying layer increases in thickness, the need for a greater amount of light to induce germination also increases, or in other words, the germination percentages in the dark decrease. This attains a maximum in the seed of *Plantago major,* where this layer is quite definite and obvious. Thus, it can safely be supposed that a direct relationship may exist between the thickness of this pigmentcarring layer and the germination light requirements of the seeds.

The interference of the seed coat with the germination has been interpreted as taking place through any of the following routes:

a) Mechanical, preventing the enlargement of the embryo.

b) Hindering light from entering the embryo.

c) Preventing some sort of inhibitor that may be present inside the seed from being leached out (ROBERTS, 1969).

d) Limiting certain oxidation processes from being completed. IKUMA and THIMANN (1963) have attributed the promoting effect of red light on the germination of lettuce seeds to the influence of this factor on the production of a set of enzymes that enable the radicle to elongate outwards through the seed tissue.

GUGLIADA et al., (1967) working with the photoblastic seeds of *Datura ferox,* stated that the oxidised products with whose production the seed coat interferes would permit the photomechanism to become operative or, once this has been completed, to overcome the blockage imposed by the "inhibitor".

EDWARDS (1968) investigated the dormancy of charlock *(Sinapis arvensis L.)* seeds, which are shown to have a testa structure similar to that of *Plantago major* seeds, and attributed this phenomenon to the phenol and mucilage content of testa hindering the diffusion of oxygen into the tissue of the embryo.

That the seed coat may completely block the germinationpromoting effect of red light was demonstrated by SANCHEZ et al., 1967.

Then, it can be stated that in the light-sensitive seeds of *Plantago* and similar species, the seed coats may interfere either directly, preventing light from entering the embryo, or indirectly, preventing some light-sensitive oxidationinhibiting products from being leached out, therebly retarding germination in the dark.

WAREING (1966) reports that it is difficult to see what adaptive value arises from light-sensitivity in seeds and that the more frequent light requirements mean that germination can only occur on the soil surface. He adds that although it is difficult to see any very marked adaptive in light-sensitivity, its ecological importance is unquestionable, especially in the germination of weed seeds following agricultural disturbance of the soil.

TADROS and REZK (1970) have put forward a working hypothesis as regards the interspecific phylogenetic relations in four species of *Plantago*. From that hypothesis it was proposed that *Plantago major* by virtue of its mesophytic character moist

habitats and subcosmopolitan distribution, may be regarded as the ancient as compared with the other non-mesophytic species of *Plantago*. e.g. *P. squarrosa* (annual psammophite) and *P. crassifolia* (perennial halophite).

If we non try to correlate the evolutionary tendencies of the species in the light of the working hypothesis mentioned above, it can be said that there is a parallel decrease in the sensitivity to light of the seed with the progress of evolution.

The seeds of *P. major* the more ancient mesophytic species, proved to be acutely light-sensitive, containing a light-impervious layer, the palisade or malphighian layer, that is assumed to be the site of preventing light from entering the seed. As evolution proceeds and new species develop from the more ancient, a decrease in the light-sensitivity is manifested. This may be supposed to have proceeded through the following parallel lines:

a) Change of seed shape from the small closed triquetrous *(P. major)* to the larger, more open plano-convex *(P. crassifolia)* to the concave-convex boat shaped *(P. squarrosa)* seed.
b) Decrease of pigmentation of the seed coat and the disappearance of the palisade light-impervious layer, paralleled by the decreased sensitivity to light.

These conclusions, however, need further verification and evidence through other cytotaxonomic, morphologic and genetic studies.

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RAPID PRODUCTION OF PROTEIN-FORMING AMINO ACIDS WITH THE AID OF WATER STRESS AND PHOTOSYNTHESIS I. THE "PROLINE PATHWAY" OF AMINO ACID METABOLISM

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Abstract

Depending on their response to water-stress, it is possible to classify plants in two groups: (1) types accumulating free proline, and (2) those not accumulating proline. The differentiation can be made on flowering (microsporogenesis) by the method of the rapid "live-wilting" of the isolated leaves and shoots. Proline accumulation in the leaves in the event of water-deficit is advantageous, for it significantly increases the amount of strongly bound water, and of the protein-forming amino acids proline has by far the highest water-solubility and can therefore remain in an active state.

On oxidative, acidic hydrolysis, all of the protein-forming amino acids decomposed with the exception of proline, i.e. it is very stable. When proline is formed from glutamic acid, the reducing energy resulting from the photosynthesis is stored, and after the cessation of the water-deficit is released again when glutamic acid is re-formed. Proline compensates the 2,4-DNP-induced respiration-inhibition, and of the amino group donors (glutamate, glutamine, aspartate, asparagine, alanine, arginine, etc.) least inhibits the growth and division of the cells when in high concentration. By the "artificial live-wilting" of the isolated leaves and shoots their free amino acid content (and protein value) can be increased.

Introduction

Studies have been made of the water-deficit of field-grown plants in the entire process of development of strong water-stress, from the beginning of the water-deficiency (PÁLFI, 1968a, b; PÁLFI and BITÓ, 1970; PÁLFI et al., 1973; PÁLFI and JUHÁSZ, 1969, 1971). The contents of water, dry matter, carbohydrate, soluble total protein and free protein-forming amino acids were investigated in leaf samples taken daily. The results were controlled with a regulated water-supply in breeding vessels. The reverse process was also carried out: detailed analyses were performed after the water-supply was once established at the optimum level by irrigation at the time of strong soil-dryness.

Individuals of 80 cultivated plant species belonging to 14 families were examined. It was found that at the time of "development" of the water-deficiency the synthesis of free amino acids does not decrease, and indeed the formation of amides and some protein-forming amino acids even increases. However, proteins are not formed from free amino acids, or only as much protein is synthetized as decomposes. For this reason the plasm accumulation and the cell division come to a stop, while the most characteristic vital activities of the plants, the flow (internal movement) of the dissolved substances and the growth, decrease and then cease (ACEVEDO et al., 1971; BRITIKOV and LINSKENS, 1970; SAVITSKAYA, 1967). It is known that, even up

to a 60—70% water-deficit of the leaves, the photosynthesis does function, but to a decreased extent (ACEVEDO et al., 1971; COWAN and TROUGHTON, 1971; REDSHAW and MEIDNER, 1972; SANTARIUS and ERNST, 1967). Since the synthesis of starch, proteins and nucleic acids (BOURQUE and NAYLOR, 1971; DOVE, 1967) stagnate, of the products of photosynthesis, besides the major amino acids, mainly the amides, the essential amino acids, and particularly proline, are stored to greater extents up to the exhaustion of the nitrogen reserves (PÁLFI, 1971b; PÁLFI and BITÓ, 1970; PÁLFI and JUHÁSZ, 1971). At such time the total protein-forming amino acid content of the leaves exceeds even 10% of the dry matter.

In the course of the analysis of the plants organ by organ it was discovered, as has also been found by others (BARNETT and NAYLOR, 1966; PÁLFI, 1968a; PÁLFI and JUHÁSZ, 1969; STEWART et al., 1966), that the amino acids accumulate only in the parts containing chlorophyll, and not in the roots, no matter how severe the water-deficiency. In the case of a water-deficit, therefore, a part is also played in the synthesis of amino acids by the assimilation of carbon dioxide. Thus, if intact plants grown under normal conditions in breeding vessels filled with soil are kept in the dark for several days, with simultaneous withdrawal of water, the protein and free amino acid contents of the leaves decrease rapidly, and proline does not accumulate either (PÁLFI, 1968a, b; PÁLFI and BITÓ, 1970).

The extensive accumulation of the free amino acids of the leaves is a particular mechanism of defence against the drying-out. With their active groups, the amino acids bind a large number of water molecules, whereby further water-loss is decreased. It is also favourable for the water-deficient plant that of all the protein-forming amino acids proline is the most highly soluble in water. It is interesting that in the event of a water-deficiency proline is formed from glutamic acid (BARNETT and NAYLOR, 1966; PÁLFI and BITÓ, 1970; PÁLFI and JUHÁSZ, 1969; STEWART et al., 1966), but its solubility in water is fifty times higher than that of glutamic acid. When the cells lose water, therefore, it is not precipitated to become inaccessible.

Result and Discussion

In the course of the experiments it was found that if the protein-forming amino acids are subjected to hydrochloric acid hydrolysis, in the presence of nitrate or some other oxidant, then all of the amino acids with the exception of proline decompose within 24 hours. In this respect, therefore, proline is the most stable amino acid. This has been reported previously too (EPPENDORFER and RILLE, 1973).

With oat-coleoptile and pea-segment tests, and with wheat and *Sinapis alba* germination experiments, the high concentration of proline ($3{,}5\times10^{-2}$ M), compared to those of glutamic acid and glutamine (which frequently appear as reserve), asparagine, alanine, and arginine, has the lowest inhibiting effect on the growth and division of the cells (PÁLFI et al., 1973). Indeed, in the event of injurious effects the free proline stimulates the normal respiration of the cells (BRITIKOV and LINSKENS, 1970; PÁLFI, 1971b). The formation of proline from glutamic acid is a several-step process requiring energy and ATP. In the case of a water.deficit, proline did not form in the leaves if a preliminary spraying was carried out with 2,4-DNP (10^{-3} M), since the oxidative phosphorylation and the ATP synthesis were inhibited (PÁLFI, 1971b).

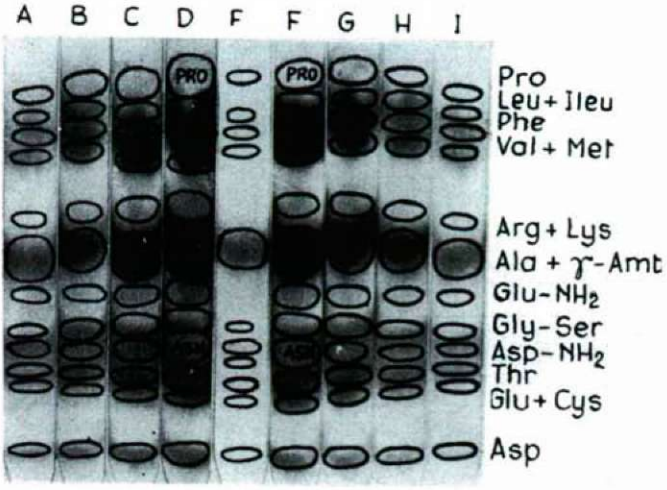

Fig. 1. Free amino acids of shoots of pea plants ("Express" variety) grown in soil-filled breeding vessels. On the effect of an increasing water-deficiency the amino acid content of the shoots increases to several times that of the control (strip E), supplied continuously with the optimum water.
A, B, C, D = 1, 2, 3 and 5 days, respectively, after cessation of irrigation. In soil suddenly saturated to the optimum water content by re-irrigation, the turgor of the shoots is re-established within a few hours, but the extremely high amount of accumulated free amino acids decreases to the normal level only after several days. F, G, H, I = 1, 3, 5 and 7 days, respectively, after re-irrigation. (The extracts refer to identical weights of dry matter.) The solvent of the paper chromatogram was phenol-water (4:1), and the developer was ninhydrine.

After the cessation of the water-deficiency the proline is reconverted to glutamic acid, and the incorporated energy is released (BRITIKOV and LINSKENS, 1970; PÁLFI, 1971b, 1972; PÁLFI et al., 1972; STEWART, 1972). This reducing energy is employed by the cells in their commencing building processes. In addition, proline is an important consitituent of the proteins of the growing cell wall, but after incorporation is converted to hydroxyproline (ROBERTS and NORTHEOTE, 1972; SAVITSKAYA, 1967). Then again the proline not only reserves energy in the critical period, but, together with the other amino acids, is the most important "protein-forming raw material" of the commencing growth processes.

The results of tissue-culture nutrient-medium experiments indicate that the proline also plays a role in the induction of the flowering (BOUNIOLS and MARGARA, 1971). A significant amount of proline can be found in the pollen too, and controls its fertility (BRITIKOV et al., 1965; SAVITSKAYA, 1967).

After the rapid saturation of the dry soil of the wilted plants with water, although the turgor of the leaves is reestablished within a few hours, the high amino acid level, and particularly that of proline, is normalized only slowly, within 6—7 days.

It turned out that not all plants accumulate proline to an extremely high extent in the case of a water-deficit. For example spinach, sugar-beet, fodder-beet, sorrel, lettuce and maize proved not to be "proline-type" plants (PÁLFI et al., 1973).

The amino acid metabolism can be considered as of the "proline-type" if, as a result of a severe water-deficiency in the leaves, the proline increases to above

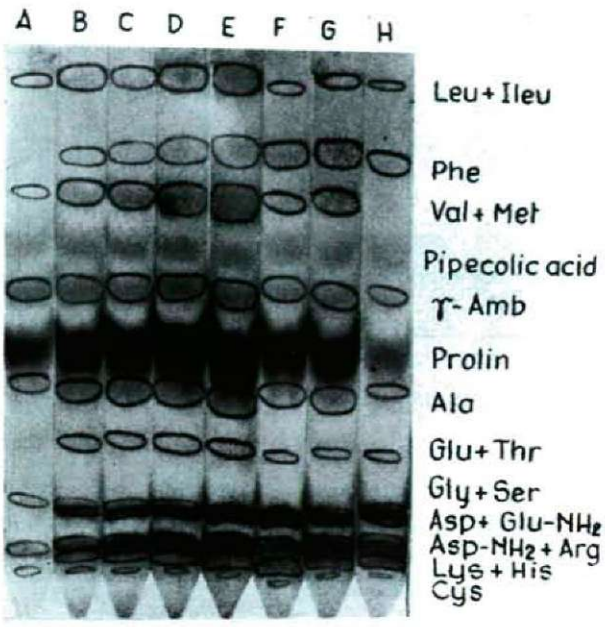

Fig. 2. Free amino acid changes in the leaves of breeding-vessel paprika plants. On the effect of a water-deficit of some days the amino acid content of the leaves increases to several times that of the irrigated control. This is shown particularly well by the proline spots (the largest and darkest spots).
A, B, C, D, E=extracts of leaves of plant not irrigated for 1, 2, 3, 4 and 5 days. After re-irrigation, the turgor of the leaves is re-established within a few hours ,but the "proline-type" amino acid accumulation decreases to the normal level only after several days. F, G, H= =2, 4 and 8 days after saturation of the soil with water to the optimum level. All samples refer to the same weight of dry matter. The solvent was n-butanol-acetic acid-water (3:1:1), and the developer was isatine.

1% of the dry matter. Other characteristics of the "proline-type" are relatively lower glutamic acid, glutamine, γ-aminobutyric acid and arginine accumulations and, apart from the Leguminosae family, the low asparagine level too. (This definition is arbitrary, for there are also "transitional species", e.g. bean.)

It has been established that 60—70% of the soft-stemmed (herbaceous) cultivated plants are of the proline-type. The entire Solanaceae family and most genera of the Leguminosae, Cruciferae, Compositae and Graminae families exhibit proline metabolism. Although the non-proline-types are characterized by a lower total amino acid level, that of the essential amino acids is higher. The water-deficit amino acid composition shows that the "non-proline-type" plants belong mainly to species of the Chenopodiaceae and Polygonaceae families. If it is desired to study the change in metabolism induced by the water-stress, it is first worthwhile to decide whether the plant examined is of the proline-type or not. This is particularly so if the pathways and enzymes of the amino acid and proline changes are investigated.

A simple and fast method has been developed for the demonstration of the proline-type (PÁLFI et al., 1973; PÁLFI and JUHÁSZ, 1971). It has also been proved that proline accumulates to an extreme extent in the leaves only as a result of water-

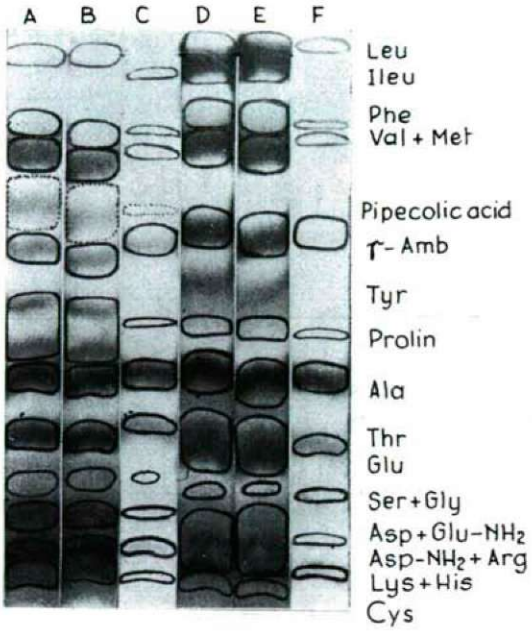

Fig. 3. The considerable increase of the free amino acid content accompanying "live-wilting" of the excised shoots and isolated leaves, with constant illumination for 2—3 days.
A, B=amino acids of "live-wilted" lucerne shoots. C=amino acids of lucerne shoots fixed immediately (not wilted) on isolation (control). D, E=amino acids of isolated "live-wilted" spinach leaves. F=amino acids of spinach leaves fixed immediately (not wilted) on isolation (control.) Every sample refers to the same weight of dry matter.
On the effect of the live-wilting the amino acid content increased to 3—4 times that of the control. In lucerne the proline was enriched to 50 times that of the control. The solvent was n-butanol-acetic acid-water, and the developer ninhydrine.

deficiency; this phenomenon can be observed in all the developmental phases of the plants (PÁLFI, 1968a, b; PÁLFI et al., 1972), but best of all at the time of microsporogenesis (PÁLFI, 1971b; PÁLFI et al., 1972).

The amino acid accumulation of the leaves and shoots attains the highest value, 5—12% of the dry matter of the leaves, in the course of a soil drought lasting for 3—6 weeks. In the leaves of plants provided with the optimum supply of water, on the other hand, the free amino acid comprises only 1,5—1,8% of the dry matter. Thus, if the control is taken as 100, then the accumulation is 300—600%.

A surprising turn of events: the "live-wilting" of the isolated leaves

It later emerged that in the course of the wilting of the isolated leaves, due to the water-loss, similar biochemical transformations take place as in the leaves of the intact plants as a result of a "severe water-deficiency". Nevertheless, there is a large difference between the two processes: during the development of their water-deficit, the leaves of the intact plants at first lose little water, and their water-deficiency "jumps" considerably only after the attainment of a very severe soil-dryness.

It is the reverse in the excised leaves: their water-loss reaches the maximum on the first day of the isolation; on the second and third days it decreases rapidly, and so a certain re-establishment is attained; only death is indicated by a slight increase in water loss.

The amino acid result from the samples taken daily revealed that the isolated leaves (shoots in the case of fodder-plants) attained the highest value of the accumulation of free amino acids at the time of their rapid water-loss, i.e. within 2—3 days; the equivalent value was measured for the intact plants only during the final days of a

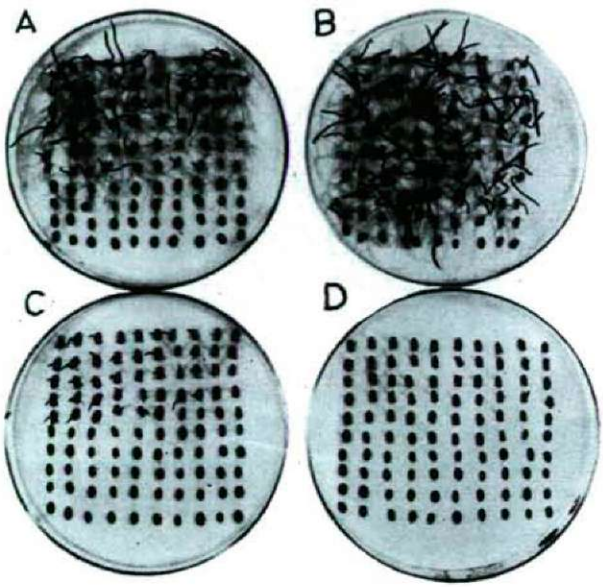

Fig. 4. The germination of wheat (variety "Bezostaya 1") in a sterile medium of a high-concentration amino acid solution ($3{,}5 \times 10^{-2}$ M) in tap water. Seeds germinating during 5 days are arranged in identical rows,
A = Proline solution B = Tap water (control)
C = Glutamine solution D = Asparagine solution
The proline medium inhibits the germination of the seeds less than amides storing NH_2 groups.

soil-drought lasting 3—6 weeks. In addition, with illumination for 2—3 days and under other opimum external conditions, there is no substantial change in the protein content either (COWAN and TROUGHTON, 1971; PÁLFI, 1971b; PÁLFI et al., 1972; TVORUS, 1970).

In the subsequent years attempts were made to find the optimum environmental conditions under which the protein-forming amino acid content of the isolated leaves could be increased artificially by a factor of several times. It was found that in the course of the "continuous water-loss" of the isolated leaves the level of accumulation of the free amino acids could be controlled by the variation of the following factors:

1) the temperature, CO_2 content and humidity of the air;

2) the degree of natural or artificial illumination (and the carbohydrate content of the leaves); and

3) the duration of the live-wilting.

When the amino acid enrichment of the leaves has attained the maximum, however, there is a rapid loss of amino acid and protein during the further live-wilting. Accordingly, in artificial live-wilting the water, dry matter, carbohydrate, total amino acid and proline contents of the leaves must be measured at 12-hour intervals, and (with functioning photosynthesis) the water-loss must be stopped (fixed) suddenly at the optimum degree. Simple and rapid methods were developed for the measurement of the above indicators (PÁLFI et al., 1973; PÁLFI and JUHÁSZ, 1971).

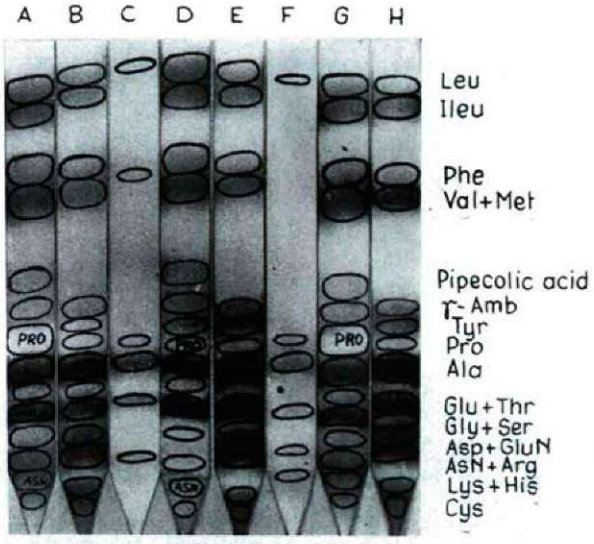

Fig. 5. Comparison of the free amino acid spectra of freshly fixed and live-wilted leaves and human tissue extracts (dividing skin tissue). With live-wilting under illumination there was a substantial increase particularly in the "essential" amino acid content of the leaves. Accordingly, the amino acid spectra of the live-wilted leaves (A, D, G) show a much greater resemblance to the amino acid composition of the human extracts (B, E, H) than do those of the freshly dried and immediately dried-out leaves (C, F). The solvent was n-butanol-acetic acid-water, and the developer ninhydrine.
A = savoy, live-wilted; B = human tissue extract; C = spinach, freshly fixed; D = spinach, live-wilted; E = human tissue extract; F = savoy, fresh; G = savoy live-wilted; H = human tissue extract.

Provoked water-deficiency and "photosynthesis operation"

The route was found for rapid biological amino acid production, and the amount thus obtained can readily be extracted by means of a simple boiling with water. With several repetitions in the cases of savoy and pea, for instance, a protein-forming total amino acid content exceeding 10% of the dry matter was attained experimentally.

It is certain, however, that other plant species and "live-wilting conditions" can be chosen, whereby even better results can be achieved. Such a method, for example, is NPK plant nutrition through the leaves on the days prior to excision, and the infiltration of the isolated leaves, or the artificial increase of the atmospheric CO_2 content and of the leaf carbohydrate content (COWAN and TROUGHTON, 1971; PÁLFI, 1971a). The presence of the carbohydrates inhibits the oxidation of proline and other amino acids (STEWART, 1972). Besides the provoked water-deficiency, therefore, there is a need for "operation of the photosynthesis" in the course of the live-wilting (COWAN and TROUGHTON, 1971). The higher CO_2 concentration of the live-wilting medium is important for two reasons:

1) it increases the intensity of photosynthesis and
2) it decreases the opening of the stomata.

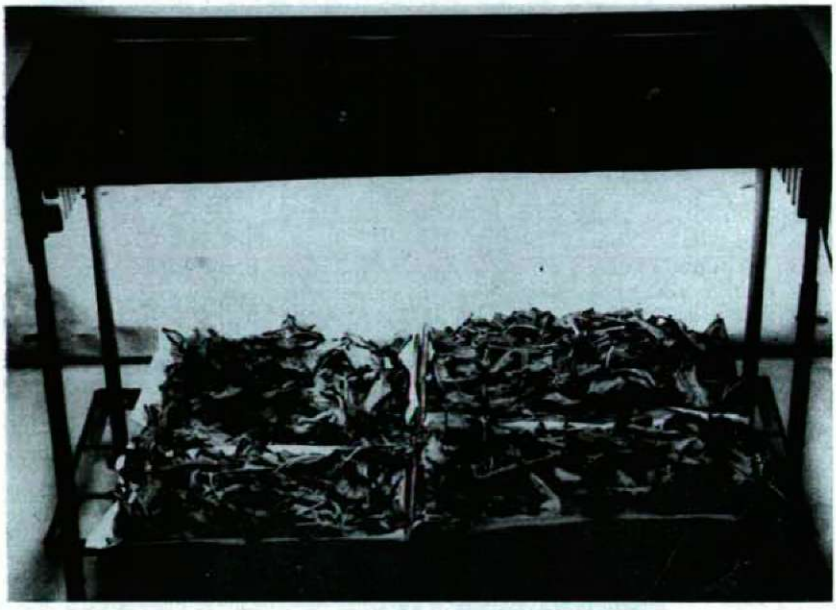

Fig. 6. Artificial increase of the amino acid content of the isolated leaves by live-wilting under laboratory conditions. The layer thickness of the spinach leaves, spread out on trays, was about 10 cm. The leaves were illuminated from above by 5 normal neon tubes at a heigh of 60 cm. In air of appropriate temperature and humidity the live-wilting combined with photosynthesis leasts 2 days. After this the material enriched in protein-forming amino acids and preserved by mild drying (dehydrated) is powdered and compacted, and packaged free from air and light.

In certain plants, with optimum light and gradual, but forceful live-wilting, the proline content of the isolated leaves can attain even 4—5% of the dry matter during 3—4 days in the course of the photosynthetic amino acid enrichment (PÁLFI, 1972). At such time, the free proline comprises 50—70% of the total amino acid. Such a plant can be regarded as a "proline works" (similarly to a "sugar works").

Table 1. Increase of free proline and total amino acid contents of isolated leaves and shoots by means of live-wilting with constant illumination. In the course of the live-wilting, with lasted 2—4 days, the total amino acid content increased 3—6 times as a percentage of the dry matter of the non-wilted, fresh control. The proline accumulation of "proline-type" plants may even increase 100 times; spinach and sorrel are not proline-type plants

PLANTS	PROLINE mg/g dry matter			TOTAL AMINO ACID mg/g dry matter		
	FRESH	LIVE-WILTED	GROWTH AS PER-CENT OF FRESH	FRESH	LIVE-WILTED	GROWTH AS PER-CENT OF FRESH
LUCERNE shoots	0,6	18,3	3 050	17,1	73,8	431
PEA shoots	0,5	21,4	4 280	20,3	124,5	613
WHEAT shoots	0,3	26,6	8 866	19,3	80,4	411
Perennial ryegrass shoots	0,4	28,1	7 025	19,2	82,4	429
SUNFLOWER leaves	0,2	23,4	11 700	12,6	41,5	329
SAVOY leaves	0,5	57,6	11 520	18,8	116,2	618
SPINACH leaves	0,4	2,2	550	16,2	68,6	423
SORREL leaves	0,3	1,7	566	15,7	47,6	303

In the repetitions of the analyses the standard deviation of the mean error is within ±8%. The live-wilting of savoy heads was performed on isolated leaves.

It is true that the sugar content of the sugar-beet is five times the proline content, but the price of proline is ten thousand times that of sugar.

It was found that 4—12 hours after the isolation the leaves have "re-adjusted" their water-loss to a certain extent. If this adaptation is disturbed by spraying with water, the decreased vital intensity (respiration, transpiration) suddenly increases. In such a case isolated leaves (spinach, sorrel and *Brassica oleracea* species) or shoots (pea, lucerne, clover and Graminae) "consume" their nutrient reserves (GENKEL' and KUSHNIRENKO, 1971; PÁLFI and JUHÁSZ, 1969).

From the aspect of the live-wilting enrichment of protein-forming amino acids, there are two essential differences between plants suitable for human nutrition (leaf-vegetables) and those used as animal fodder, as regards the processing:

1) Spinach, sorrel and *Brassica oleracea* varieties, i.e. the leaf-vegetables, must be washed several times within 3—5 hours of harvesting. During this the leaves are completely saturated with water, and the photosynthetic live-wilting begins from an "optimum physiological level". With the green foods there is no washing, i.e. no saturation with water, and thus a good result can be achieved only with plants provided with the optimum water or irrigated prior to the excision.

2) The green-vegetables generally have larger leaves, and the leaf blade too is thick and fleshy; their venation is multibranched, and so the "isolated leaves"

Table 2. Amino acid enrichment of illuminated isolated, live leaves. On the effect of live-wilting the total amount of protein-forming amino acids increased 3—5 times (in dry matter) compared to the control, which was immediately fixed and dried out on isolation. The accumulation of the essential amino acids was substantially higher (300—600%) than that of the non-essential amino acids (200—500%). Proline was an exception. (* denotes the essential amino acid) mg/g dry matter

AMINO ACIDS	SPINACH		SAVOY		SORREL	
	Fixed control	Live-wilted	Fixed control	Live-wilted	Fixed control	Live-wilted
Leucine* + Isoleucine*	0,68	7,22	0,26	4,60	0,56	5,08
Phenylalanine*	0,45	5,36	0,35	3,52	0,47	4,10
Valine* + Methionine*	0,82	7,62	0,93	5,28	0,90	7,22
Tryptophane*	0,15	0,52	0,17	0,73	0,21	0,60
γ-aminobutyric acid	1,86	5,28	2,30	4,51	1,75	3,83
Tyrosine	0,62	2,35	0,41	0,92	0,71	2,05
Proline	0,55	3,46	0,46	50,75	0,32	2,64
Alanine	2,57	6,73	2,98	5,03	2,85	5,45
Threonine*	0,47	3,46	0,85	2,68	0,54	2,92
Glutamic acid	2,90	5,58	2,37	6,10	3,07	5,16
Glycine	0,81	3,84	0,93	2,56	0,73	3,34
Serine	1,57	5,06	1,53	4,18	1,40	4,38
Aspartic acid	1,18	5,23	3,45	5,52	1,38	4,90
Glutamine	0,51	2,82	0,80	2,47	0,32	2,76
Asparagine	0,58	3,56	0,42	2,62	0,45	2,85
Arginine* + Histidine*	0,72	4,80	0,85	5,16	0,64	4,70
Lysine*	0,33	1,03	0,27	0,85	0,26	0,92
Cyst(e)ine	0,38	1,28	0,16	1,03	0,33	1,05
Total amino acid	17,15	75,20	19,49	108,51	16,89	63,95

The measurements were carried out on a "Biocal BC 200' automatic amino acid analyser. Glutamine, asparagine, proline and tryptophane were measured by separate methods.

do not lose their water content rapidly. The venation of the leaves of the green-foods, either small-leaved (clover species) or like the (Monocotyledon) Graminae, is parallel, and therefore the isolated leaves become dried out completely within one day and wilt. In the case of the green foods then the excised shoots must live-wilt. The results of our experiments show that, if it is already in the silking flowering stage, the live-wilting of maize differs substantially from these.

Preservation by mild drying

Following this, it was necessary to elaborate a preservation procedure, by means of which leaf-vegetables enriched in free amino acids retain their excellent taste and their nutriment and vitamin contents for 1—2 years. Dehydration by mild drying proved suitable (PÁLFI, 1971a, b; PÁLFI et al., 1972). Material dried to weight constancy at the required temperature is immediately powdered, and then stored protected from air and light, in a compact form. Grinding to a powder has the advantage that, compared to the coarse leaf-vegetables, more nutritive and flavouring material can dissolve up on cooking. In addition, the compacted grindings occupy little space on storage.

On the working-up of the cooking elements of the green-vegetables, it turned out that the enriched amino acid content is at the same time a concentrated flavouring material too. For this reason, our new preparations are taste and nutrient concentrates, from 8—10 grams of which, packed in foil packets, half a litre of green-vegetables can be prepared within a matter of minutes.

The new procedure is applicable to all soft-stemmed, (herbaceous) "mesophyte", Angiospermae plants in any part or place of the world.

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DATA ON THE SHOOT GROWTH-INHIBITING EFFECT OF 2, 3, 5-TRIIODIBENZOIC ACID

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Abstract

Treatment of bean seedlings with 2, 3, 5-triiodobenzoic acid (TIBA) below the cotyledon prevents the completion of the elongation of the hypocotyl and significantly inhibits the growth of the stem part above the treatment. The inhibitor decreases the fresh weight increase in parallel with the growth. The dry weight increases a little in the hypocotyl, and decreases considerably in the epicotyl.

TIBA applied to the uppermost internode inhibits the elongation of the more downward stem parts to only a small extent, but prevents the appearance of the parts above the treatment completely. Thus, not only the total length, but also the number of internodes decreases.

TIBA treatment significantly reduces the IAA content of the shoot, in the stem parts both below and above the site of treatment. The hypocotyl/epicotyl distribution ratio of the IAA content does not vary in the control as a result of the TIBA treatment. The TIBA therefore inhibits not only the transport but also the synthesis of IAA, in stem parts both below and above the treatment site.

Introduction

2, 3, 5-Triiodobenzoic acid (TIBA) is a known inhibitor of plant growth; the view is generally widespread in the literature that it specifically blocks the basipetally polar auxin transport (KUSE, 1953; NIEDERGANG—KAMIEN and SKOOG, 1956; HAY, 1956; ZWAR and RIJVEN, 1956; etc.). The majority of the authors explain the growth-inhibiting effect of TIBA exclusively in the blocking of the auxin transport from the apex towards the base, and only very few of them have dealt with its effects on the auxin content and its distribution (NIEDERGANG—KAMIEN and SKOOG, 1956; GOLDSMITH, 1968).

In the course of growth physiological experiments with bean seedlings, involving the use of TIBA, we have observed a number of phenomena which do not fit in too well with the classical conceptions of its inhibitory effect; it appeared desirable, therefore, to carry out a certain re-examination of the growth inhibition brought about by TIBA. With this aim, a study has been made of the effects of applying TIBA to various parts of the shoot on the growth of the parts of the stem above and below the site of treatment; a further investigation has been made of the influence of the inhibitor on the total auxin content of the shoot and on the apex/base distribution of the endogenous auxin (IAA).

Materials and Methods

The experiments were carried out with bean plants (*Phaseolus vulgaris* L., "White pearl"). The seeds were planted in perlite containing 70% water, and were watered with Prjanisnikov solution. The plants were grown in a green-house at 24 °C, with 16 hours of illumination daily.

TIBA in lanoline paste was used as the growth-inhibiting agent, in a concentration of 1.5%. The growth of the untreated shoots and those treated with TIBA was measured every 3 days until the 25th day after the sprouting, by determining the lengths of the internodes and also the fresh and dry weights of the shoots.

The extraction and chromatographic separation of indoleacetic acid (IAA) were carried out as described earlier (VARGA and BITÓ, 1968). In brief: a methanolic extract prepared from the tissue homogenizate was purified by shaking with petroleum ether, evaporated under vacuum, and chromatographed on a silica gel G layer with chloroform — ethyl acetate — formic acid 5:4:1 and isopropanol — 7% ammonia — water 8:1:1 as solvents. The IAA was identified by comparison of the Rf value with that of the authentic compound, by means of the colour given with the Ehrlich reagent, and from the UV fluorescence and UV absorption spectra. For quantitative determination the IAA spots were scraped off the plates, and eluted with methanol, and the concentration of IAA in the eluate was measured with a Spektromom 202 photometer at 280 nm (FLETCHER and ZALIK, 1964).

Every examination was carried out in two parallel series, repeated three times.

Results

1. Effect on the stem elongation of treating the hypocotyl with TIBA

Lanoline paste containing TIBA was smeared in a ring 2—3 mm wide onto the hypocotyl of 5-day seedlings, immediately below the cotyledon. The same number of untreated plants were left as controls. After 3, 6 or 9 days (i.e. at the age of 8, 11 or 15 days) the growths of the stem parts below and above the cotyledon were measured on the basis of three factors: the length, and the fresh and dry weights.

The effect of TIBA treatment on the stem growth is shown in Fig. 1. The untreated shoots became significantly elongated during the period of the experiment. The increase in the total length of the shoot is a result of the continuous growth

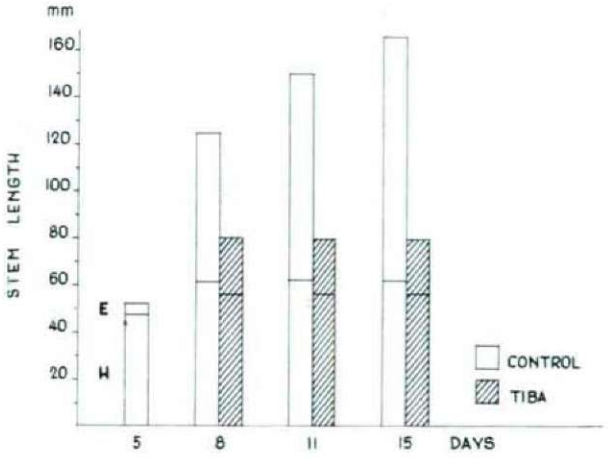

Fig. 1. Effect of TIBA treatment of the hypocotyl on the stem growth of bean seedlings. H=hypocotyl, E=epicotyl.

of the epicotyl, since the hypocotyl no longer grows after the 8th day. In the TIBA-treated shoots the total length was much lower, the growth of the hypocotyl being inhibited to a smaller extent (5—11%) and that of the epicotyl to a much larger extent (62—75%).

The TIBA inhibited the increase of the fresh weight of the hypocotyl only slightly up to the completion of the elongation, but the inhibition of the increase of the fresh weight of the epicotyl was much more significant (Table 1). The dry weight of the

Table 1. Effect of TIBA treatment on the increase of the fresh weight of bean shoots

Day	Hypocotyl			Epicotyl		
	Control g	TIBA-treated g	Inhibition %	Control g	TIBA-treated g	Inhibition %
5	0.314	0.314	—	0.121	0.121	—
8	0.566	0.510	9	0.512	0.374	27
11	0.633	0.641	—	0.879	0.536	39
14	0.583	0.590	—	1.244	0.809	35

Table 2. Effect of TIBA treatment on the increase of the dry weight of the shoots

Day	Hypocotyl			Epicotyl		
	Control mg	TIBA-treated mg	Inhibition %	Control mg	TIBA-treated mg	Inhibition %
5	26.6	26.6	—	21.6	21.6	—
8	31.6	33.3	—	75.0	48.0	36
11	37.5	39.7	—	96.6	68.6	29
14	46.0	46.8	—	164.0	111.5	32

hypocotyl of the treated seedlings did not fall behind that of the control, and in fact was even a little higher; that of the epicotyl, however, was considerably less than that of the control (Table 2).

2. Effect of TIBA applied to various internodes of the epicotyl on the elongation of the stem parts

Bean seedlings grown as described were divided into 4 groups. In the first group the lanoline ring containing the TIBA was applied to the first internode at the age of 7 days, in the second group to the second internode at the age of 10 days, in the third group to the third internode at the age of 13 days, and in the fourth group to the fourth internode at the age of 16 days, i.e. always to the uppermost internode then appearing. At 3-day intervals for 9 days after the treatment the growths of the stem parts below and above the ring were measured.

In the case of the treatment of the first internode (Fig. 2,1) it was not possible to observe the inhibiting effect of TIBA on the hypocotyl, and to only a slight extent on the first internode, for at this time these stem parts had already completely or

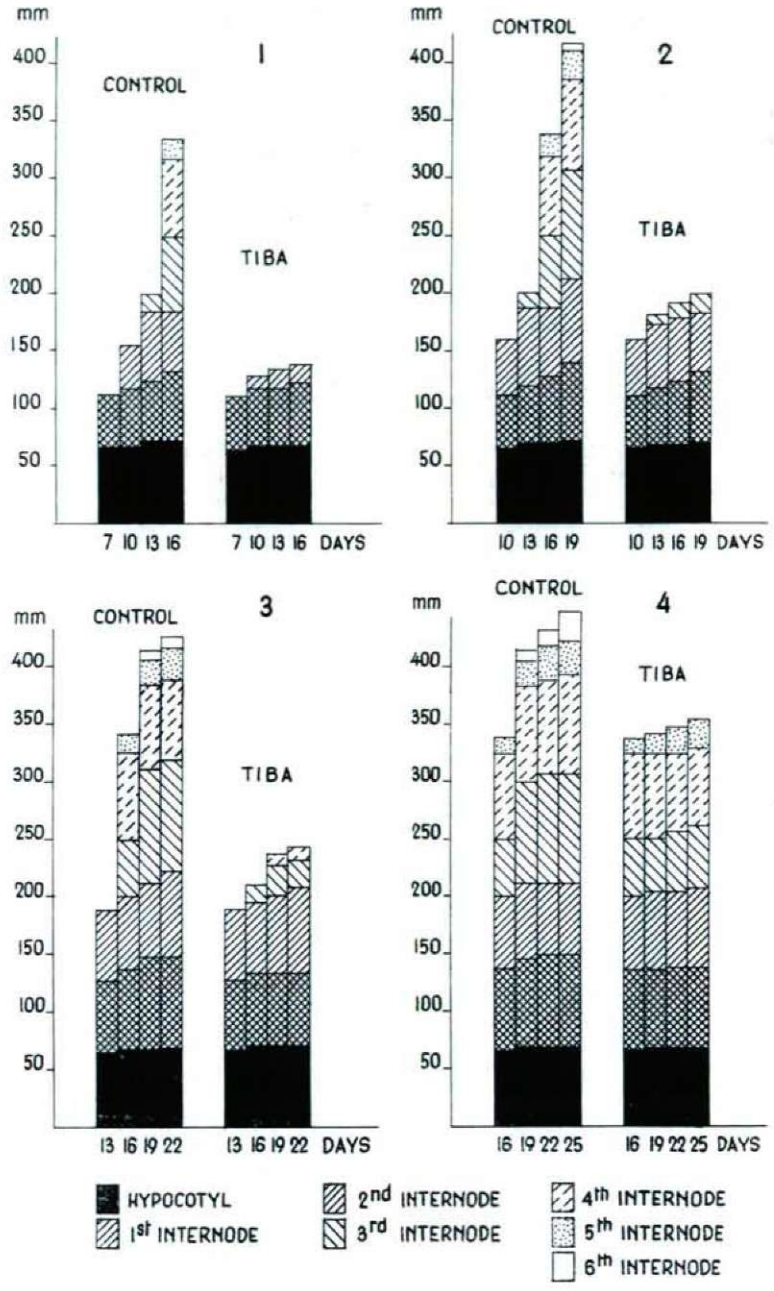

Fig. 2. Effect of application of TIBA to different internodes of the bean shoot on the elongation of the stem parts.

partially finished their elongation. On the other hand, the TIBA applied to the first internode caused a very large inhibitory effect on the development of the second internode, and completely blocked the occurrence of the following internodes. This could also be observed after treatment of the second, third and fourth internodes too: the TIBA had little effect on the elongation of the stem parts below the ring, whereas above the ring in every case only the following internode appeared to a very reduced extent, while the remaining internodes failed completely to develop (Fig. 2,2—4). It follows from this that the difference between the total lengths of the controls and the treated shoots is the smaller, the later the time of treatment of the appearing internode.

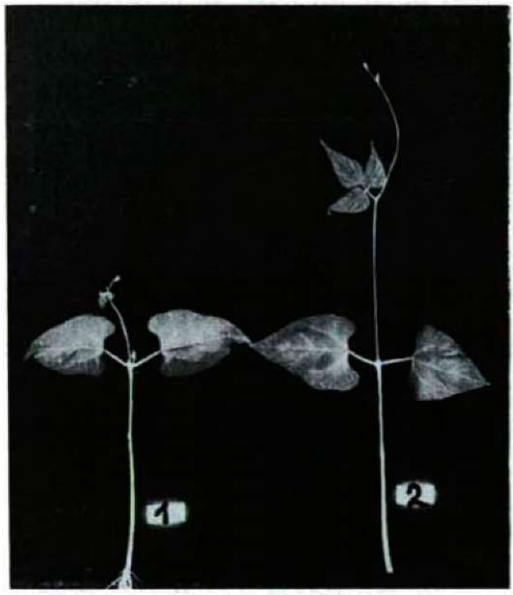

Fig. 3. Effect of application of TIBA to the first internode of the epicotyl on the shoot growth. 1 = treated, 2 = control.

Figure 3 shows the results of treatment for the first internode.

3. Effect of TIBA treatment on IAA content

The hypocotyl of 5-day bean seedlings was treated with a TIBA ring below the cotyledon, and three days later the amounts of IAA were determined in the entire shoot and in the hypocotyl and epicotyl parts separately. The results were calculated referred to one organ, and the data thus express the actual auxin contents of the shoots and the shoot parts.

The results indicate (Fig. 4) that TIBA treatment led to a marked reduction of the IAA contents of the whole shoot and the individual shoot parts (hypocotyl and epicotyl) compared to the control. This effect was somewhat more pronounced tn the hypocotyl (58%) than in the epicotyl (50%). As regards the distribution of ihe IAA content within the shoot, in the case of the control shoots less of the overall IAA content is provided to the hypocotyl (40%) than the amount remaining at the

sites of synthesis, in the apical part (60%). With TIBA treatment, although the total amount of IAA was significantly less, these ratios of the auxin distribution did not change (Fig. 4).

Discussion

When the TIBA ring was applied below the cotyledon to the stem of the 5-day seedlings, in the period following the treatment the TIBA completely inhibited the conclusion of the elongation of the hypocotyl, and kept it at the original level. At the same time the hypocotyls of the control shoots continued to grow until the eighth day, and then remained constant in length. This explains why, although the effect of the TIBA in restricting the total length of the hypocotyl is apparently slight, the inhibition calculated as a △ value attains 45—50%.

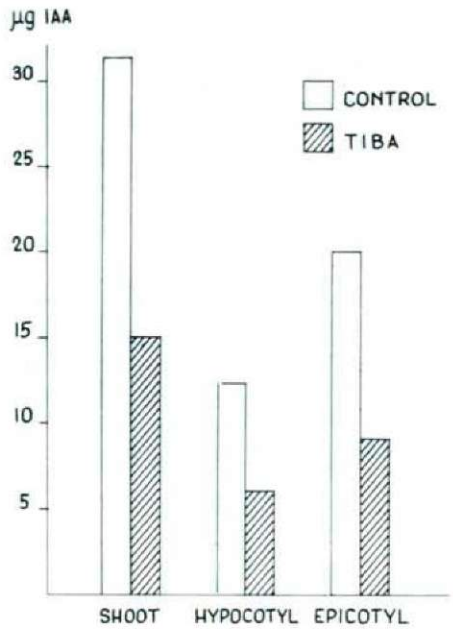

Fig. 4. Effect of TIBA treatment on the IAA content of the shoots.

The TIBA treatment exerted a striking and considerable inhibitory effect on the elongation of the stem part above the cotyledon (first internode), the analogous elongation in the control being very intensive in the experimental period. The TIBA induced inhibition of the elongation of the epicotyl stem part above the site of treatment proved to be 62, 73 and 90% in the individual measurements. This strong decrease of the elongation is in agreement with the inhibition of the fresh weight and dry matter content increase of the epicotyl.

When the TIBA ring was applied to newly appearing internodes of the epicotyl, the inhibition of the elongation of the internodes lying below the site of application was only slight, whereas the growth of those above the treated internode was com-

pletely inhibited. As a consequence of this, the TIBA treatment caused a significant decrease not only in the total length of the shoot, but also in the number of internodes, compared to the control.

As regards the effect of TIBA, the view is extremely widespread in the literature that, in accordance with the blocking of the basipetal IAA transport, inhibition of the stem growth occurs only below the site of treatment. For example, BOUCK and GALSTON (1967) report that application of TIBA to the third internode of pea stimulated the elongation of the stem above the ring, but significantly inhibited the growth of the stem parts below the ring. All this is explained by the accumulation above the ring of the auxin amounts migrating downwards under polar effects. TANIMOTO et al. (1967) similarly treated the middle of the third internode of pea shoots with TIBA; the upper half of the internode elongated strongly, whereas the lower half hardly grew. According to the authors, the cause of the phenomenon is almost certainly the uneven distribution of the IAA originating from the apex in the two halves of the internode, as a consequence of the blocking of the IAA transport by the TIBA. In contrast with these publications, our results show that the inhibitory effect of the TIBA on the stem elongation is definitely exerted upwards from the site of treatment. Thus, the blocking of the basipetal auxin transport can not be the only reason for the effect of TIBA.

A TIBA ring applied beneath the cotyledon to the young shoots of the seedlings significantly inhibited the increase of the IAA contents of both the hypocotyl and the epicotyl, i.e. the stem parts not only below, but also above the ring. These data are likewise in contrast with the results of certain publications. A number of authors have reported that the application of a TIBA ring to the stem or a stem-segment retains the bulk of the auxin in the apical part of the stem, and inhibits its accumulation in the basal part below the treatment (HEJNOVICZ and TOMASZEWSKI, 1967; LEOPOLD and FUENTE, 1967; HERTEL and FLORY, 1968).

In our experiments the TIBA treatment did not change the normal apex/base ratio of the total amount of auxin in the shoot, i.e. it inhibited the increase of IAA in the parts below and above the ring to roughly the same extent. In their investigations on tobacco stem segments, NIEDERGANG—KAMIEN and SKOOG (1956) similarly observed an inhibitory effect of TIBA on the total auxin content; study of the distribution of the amount of endogenous auxin within the stem segment, however, revealed a shift of the apex/base ratio in favour of the base.

Our data lead to the overall finding that the TIBA inhibits not only the transport of IAA in the treated shoots, but also the auxin content (synthesis). This dual effect is manifested both in the stem parts below the ring and in those above it. In the event of the application of TIBA in other concentrations (0.5, 1.0 and 2.0% inhibitor), its growth-inhibitory effect was exerted in a similar way.

The details of the mode of the TIBA effect observed by us require and are worthy of further investigations.

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ION UPTAKE AND CELL-MEMBRANE BEHAVIOUR OF SYNPRAN N AND DACTHAL HERBICIDE-TREATED RICE PLANTS

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Abstract

A study was made of the effects of Synpran N and Dacthal herbicides on the ion uptake, leakage and change of free amino acids of young rice plants in nutrient solution with the help of an isotope technique. The isotopically labelled solution contained different concentrations of Synpran N or Dacthal herbicides. Synpran N is 34% dichloropropion-anilide, while Dacthal is the dimethyl ester of tetrachloroterephthalic acid.

It was established by investigation of Synpran N that 10^{-5} M and 10^{-6} M concentrations do not give rise to unfavourable effects on the K-ion uptake compared to the control. At 10^{-4} M concentration a slight inhibitory effect can be observed, while at 10^{-3} M the ion uptake practically ceases. The situation is similar, to a certain extent, to the uptake of phosphate ion. In contrast with the Synpran N examinations the ion uptake is not inhibited markedly by Dacthal, even at a concentration of 10^{-3} M.

From the K-ion leakage experiment it can be established that the rate of efflux tends to inrease with the Synpran N concentration. The free amino acid content of the roots after a four hours' treatment with 10^{-3} M and 5×10^{-4} M Synpran N was very low due to damage to the cell-membranes.

General growthinhibition of the roots is caused by 10^{-3} M and 5×10^{-4} M Synpran N concentrations, while Dacthal causes a striking disturbance even at 10^{-6} M concentration.

Introduction

An investigation was made earlier to study the ion uptake of fungicidetreated rice seedlings. It was established that the fungicide Kitazin effectively inhibited the ion uptake and growth at higher fungicide concentrations, while at lower concentrations the effects exhibited were not injurious, but rather favourable (ZSOLDOS, 1973).

There is no clear understanding why biologically active compounds, among them herbicides, modify the uptake of mineral elements (AUDUS, 1964; FREAR and SHIMABUKURO, 1970). Changes in cell-membrane permeability and the rate of cell respiration of treated plants probably also play an essential role in this process.

It is clear that this question is very important from both theoretical and practical points of view, because of the toxic or enhancing effects of herbicides on mineral uptake. For this reason ion uptake experiments were carried out with rice plants with different herbicides in the expectation of clearing up some of the above problems.

Materials and Methods

Excised rice roots and intact rice plants *Oryza sativa* var. *japonica* were used throughout these experiments. Seeds were disinfected for one minute with 1% $HgCl_2$ solution, rinsed in running tap water for 4—5 hours and allowed to germinate on filter paper in Petri dishes. Following germination, the material was transferred to stainless steel screens supported in 15-litre polyethylene containers or one-litre glass containers filled with 5×10^{-4} M $CaSO_4$ solution. The entire container was covered by a sheet of nylon.

The seedlings were grown in the dark at 25 °C for 3 days. After this, the nylon was removed and the seedlings were exposed to artificial light at 10 thousand Lux for 16 hours a day, still at 25 °C. The plant were used for ion uptake experiments when they were 7—8 days old, the roots then being about 6 cm long.

Before the start of a short-time ion uptake experiment, the whole roots were excised just below the stainless steel screen, 3 g samples were transferred to 250 ml beakers and washed with distilled water. The samples were then placed in 500 ml aerated, isotopically labelled absorption solution containing different concentrations of Synpran N or Dacthal. The active ingredient of Synpran N is 34% dichloropropionanilide, while that of Dacthal is the dimethyl ester of tetrachloroterephthalic acid. In the following, the concentration values given refer to the pure active ingredient.

The K-ion uptake studies were carried out in 10^{-3} M KCl solution using Rb^{86} as tracer. The uptake of phosphate ion from 5×10^{-4} M KH_2PO_4 solution was studied with the help of P^{32}. Uptake vs. time graphs were obtained at different concentrations of herbicides.

The root samples were removed from the absorption solution at different intervals and rinsed three times in distilled water. The roots were then dried on filter paper for two hours at room temperature, and put into aluminium dishes for determination of the activity of the samples. The results are given in μM/g dry weight. The pH of the absorption solutions was adjusted to 6.3—6.4 by adding 0.1 N NaOH or HCl and after the absorption period it was again checked.

In the experiment on K-ion loss from tissues affected by treatment with different concentrations of herbicide, 3 g root samples were first left to stand 40 minutes at 23 °C in 600 ml 10^{-3} M KCl+ $+5\times10^{-4}$ M $CaSO_4$ solution containing Rb^{86} as tracer. They were then rinsed in 3×350 ml distilled water and put into 500 ml 5×10^{-4} M $CaSO_4$ solution at 23° C containing herbicide in different concentrations. A root sample was taken from the various solutions every 10 minutes, washed as described above, and prepared for activity measurement.

The difference between the activities at the beginning and end of the leakage experiment was considered to be equivalent to the efflux. In our opinion the data obtained in this way also show the change in the permeability of the membranes. All experiments were repeated at least two or three times and the trends were indentical, showing the effects to be due to sample treatment and not sample difference.

In the experiments on the effects of different Synpran and Dacthal concentrations on the growth and the change of the free amino acid content of the roots, the plants were put in Hoagland nutrient solution containing herbicide in different concentrations. After 4—5 days' treatment the free amino acid content of the roots was determined by the standard paper-chromatographic method. The amino acid content of fresh roots represents the fraction soluble in 70% ethyl alcohol.

Results and discussion

1. Investigation with Synpran N

The K-ion uptake by excised roots in the presence of different concentrations of Synpran N is visible in the graphs of Fig. 1. The graphs clearly indicate that lower (10^{-5} M and 10^{-6} M) Synpran N concentrations do not give rise to unfavourable effects compared to the control. At higher concentrations, e.g. 10^{-4} M, a slight inhibitory effect can be observed, while at 10^{-3} M the ion uptake practically ceases.

As seen in Fig. 2. the situation is similar to a certain extent with the uptake of phosphate ion; the difference is that a slight inhibitory effect is found at a slow as 10^{-5} M, while, in marked contrast, at 10^{-6} M the herbicide exhibits a stimulatory effect.

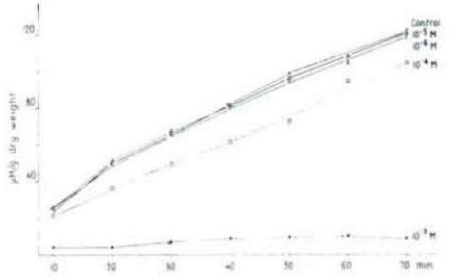

Fig. 1. K-ion uptake from 10^{-3} M KCl solution at different Synpran N concentrations.

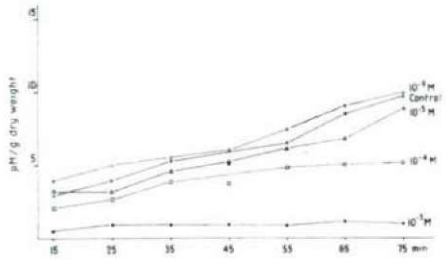

Fig. 2. Phosphate ion uptake from 5×10^{-4} M KH_2PO_4 solution at different Synpran N concentrations.

With Synpran N too, a study was made of the effects of herbicide treatment on the ion leakage. The results are illustrated by the data of Fig. 3. It can be seen that the rate of efflux tends to increase with the Synpran N concentration, a definite increase of rate being found for 5×10^{-4} M Synpran N, and a much more marked one for 10^{-3} M Synpran N.

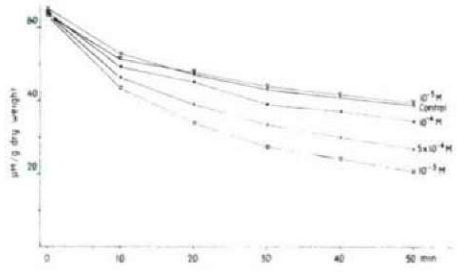

Fig. 3. K-ion leakage by roots on different Synpran N treatments.

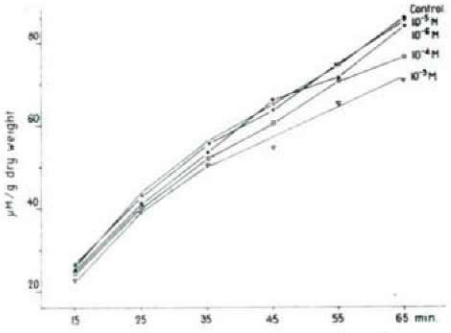

Fig. 6. K-ion uptake from 10^{-3} M KCl solution at different Dacthal concentrations.

At lower Synpran N concentrations the ion-leakage is not significantly different from that of the control. That is to say, in the presence of 10^{-4} M, or 10^{-5} M Synpran N, where the roots could absorb ions essentially in a unidirectional fashion, there is little if any measurable efflux. Thus, the membrane separating the cell interior from the external medium, the plasmalemma, is highly impermeable to diffusive permeation by inorganic ions.

In a normal healthy tissue, the membrane acts as a barrier to free diffusion and exhange of ions (EPSTEIN, 1972). However, when the membranes responsible for this retention are injured, as was found at high Synpran N concentrations, there is a rapid leakage of ions and even other compounds out of the tissue following their own diffusion gradients. From the above findings, the conclusion can be drawn that the effects of biologically active compounds in high concentrations result in

an extensive disorganisation of the cell membranes and the root tissue becomes "leaky".

In addition to the ion uptake experiments, a study was also made of the effect of Synpran N on the free amino acid content of the roots. Fig. 4 a shows a chromatogram obtained from alcoholic extracts of roots treated with various concentrations of herbicide.

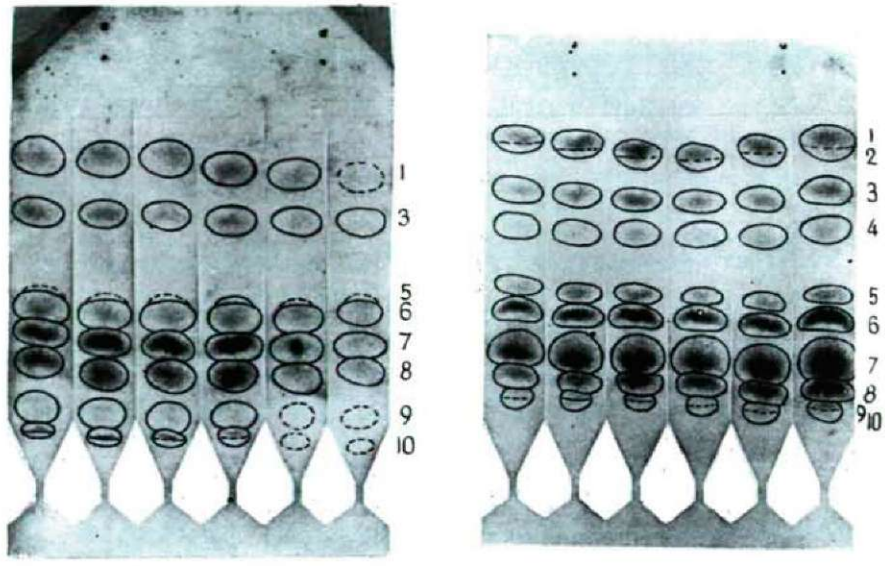

Fig. 4. a. The effect of a four hours' treatment with Synpran N on the free amino acid content of roots. From left: control (at the beginning of the investigation), control, 10^{-5} M, 10^{-4} M, 5×10^{-4} M and 10^{-3} M Synpran N. (1. leucine, 3. valine, 5. tyrosine, 6. alanine, 7. glutamic acid, 8. glutamine+aspartic acid+glycine, 9. asparagine, 10. histidine, lysine).

b. The effect of a four days' treatment with Dacthal on the free amino acid content of roots. From left: control, 10^{-7} M, 10^{-6} M, 10^{-5} M, 10^{-4} M and 10^{-3} M Dacthal (1. leucine, 2. isoleucine, 3. valine, 4. γ-aminobutyric acid, 5. alanine, 6. glutamic acid, 7. glutamine+aspartic acid+glycine, 8. asparagine, 9. histidine, 10. lysine).

It can clearly be seen that at 10^{-3} M and 5×10^{-4} M Synpran N concentrations there is a very marked decrease of the free amino acid content, presumably due to damage increasing the cell membrane permeability, resulting in leakage of the free amino acids from cells.

It is remarkable that at 10^{-4} M Synpran N concentration some of the free amino acids are higher than in the control, probably due to herbicide treatment resulting in an unfavourable effect on the nitrogen metabolism leading to a lower formation of protein.

The ion uptake experiments were supplemented with growth experiment, the results of which are shown in Fig. 5. It can be seen that a general growth inhibition is caused only by the 10^{-3} M and 5×10^{-4} M Synpran N treatments. It must be emphasized that the length of the roots at 10^{-3} M and 5×10^{-4} M Synpran N

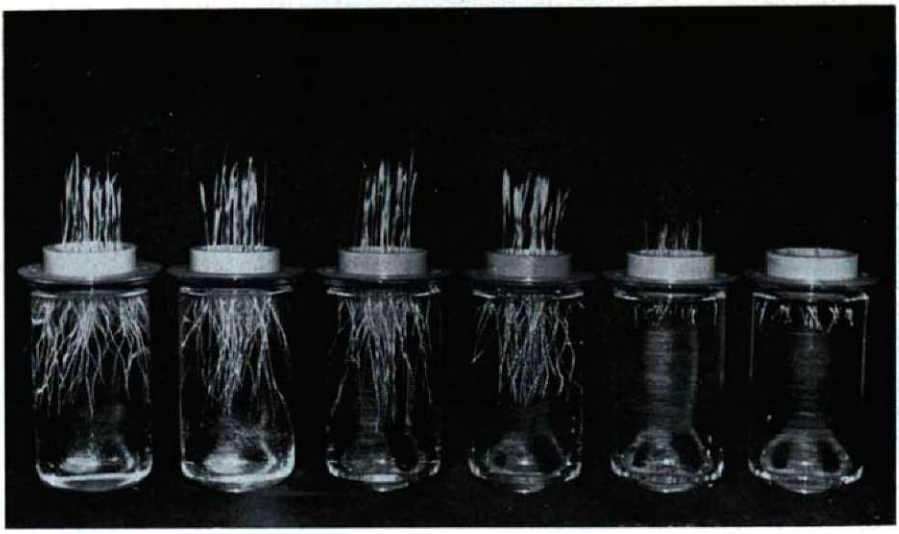

Fig. 5. The effects of a four days' treatment with Synpran N on the growth of rice plants. From left: control, 10^{-6} M, 10^{-5} M, 10^{-4} M, 5×10^{-4} M and 10^{-3} M Synpran N

were the same at the beginning of the experiments as at the end of them, i.e. no change took place during the 4—5 days.

The formation of new roots is prevented at 10^{-3} M and 5×10^{-4} M Synpran N concentrations, thereby demonstrating the influence on the morphogenesis. STRUBBE and FELLENBERG, (1972) have reported the inhibition effects of some herbicides on root formation. It is noteworthy that although 10^{-3} and 5×10^{-4} M Synpran is indisputably toxic, a herbicide treatment of 4—5 days does not destroy rice plants.

2. Investigation with Dacthal

Dacthal, a pre-emergent herbicide, kills many weeds and annual grasses in rice fields. This herbicide is not used extensively, but experiments have recently been made with it on rice since it appears to be effective againts *Echinochloa crus galli*. It is a root herbicide, and thus seemed very suitable for our ion uptake studies.

Fig. 6 shows K-ion uptake in the presence of various concentrations of Dacthal. It is immediately obvious that in contrast with the Synpran examinations the ion uptake is not inhibited markedly, even at a Dacthal concentration of 10^{-3} M. This is all the more surprising, for at the same time there is a striking disturbance of the root growth at very low (10^{-6} M) concentration (Fig. 7).

In our opinion the effect of Dacthal on root elongation can be explained in two ways. First, on Dacthal treatment an endogenous production of ethylene can occur and inhibits auxin transport and root elongation. Secondly, Dacthal treatment itself may inhibit auxin transport. Naturally, the role of Dacthal in the inhibition of root growth is subject to further investigation. It is known, however, that the endogenous production of ethylene causes root elongation disturbances (CHADWICK and BURG, 1970; PRATT and GOESCHL, 1969).

From the above-mentioned facts it appears that Dacthal, though having a solubility in water of less than 0.5 ppm, still causes a remarkable physiological

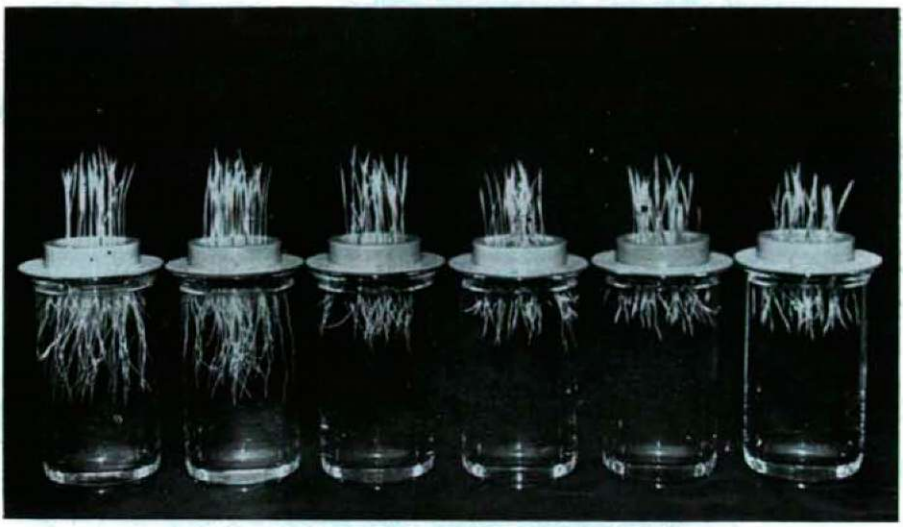

Fig. 7. The effect of a four days' treatment with Dacthal on the growth of rice plants. From left: control, 10^{-7} M, 10^{-6} M, 10^{-5} M, 10^{-4} M and 10^{-3} M Dacthal.

disturbance. At the same time it is noteworthy that Dacthal, in contrast with Synpran N, does not cause any membrane damage, as proved by the free amino acid investigations too (Fig. 4b.)

The free amino acid examinations demonstrated that some of them increased, especially at 10^{-3} M Dacthal concentration. In our opinion this result can be explained in that Dacthal does not disturb the uptake of nitrogen particularly. Only nitrogen transport and the synthesis of some nitrogen compounds may suffer damage, resulting in an increase of free amino acids in the roots.

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CHROMOSOME CHANGES IN ALLIUM CEPA AND VICIA FABA PLANTS

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Abstract

Attempts were made to produce polyploid forms in broad bean *(Vicia faba)* with colchicine, and in onion *(Allium cepa)* with colchicine and ethyl methanesulphonate.

The results indicated that a 1-hour colchicine treatment stimulated the course of the division cycle in the root meristem cells of *Allium cepa*, while the same treatment led to tetraploidy in the root meristem cells of *Vicia faba*.

On the action of colchicine the chromosome number is doubled in 50% of the plants treated. Phenotype aberrations were observed on the application of colchicine to *Sorghum* seedlings (BERAHO and OLEMBO, 1971). A colchicine emulsion affected the mitotic cycle, and caused autotetraploidy and giant growth (DHILLON, 1970; MACLEOD, 1971; 1972). Ethyl methanesulfonate and colchicine gave rise to polyploidy in pea (DUDITS, 1971). Attempts were made in our experiments to produce polyploid forms with colchicine in broad-bean *(Vicia faba)* plants, and with colchicine and ethyl methanesulfonate in onion *(Allium cepa)*.

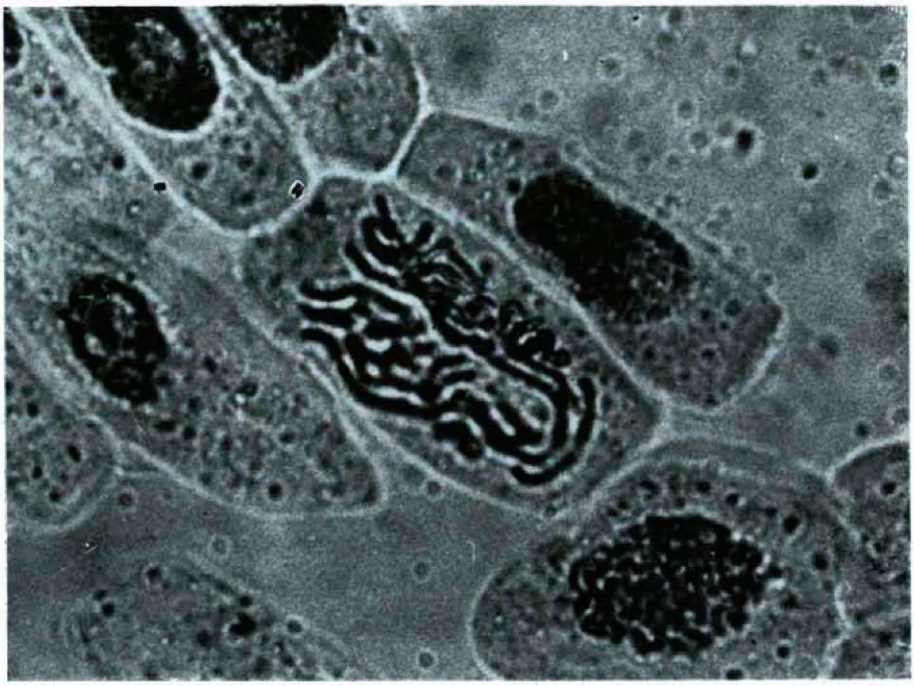
Materials and Methods

Pre-swollen and germinating seeds of *Vicia faba* and *Allium cepa* were treated for 1 and 10 hours with a colchicine solution containing 1 or 5 mg per 100 ml deionized water. In the case of the onion seeds 0.1 and 1% ethyl methanesulfonate solutions were also used. The treated seeds and seedlings were kept in a 23 °C thermostat. In another series of experiments both plants were pre-treated with a 1 mg/1000 ml kinetin solution. Colchicine-treated broad-bean plants were grown to seed-bearing in the field. Under semi-conditioned circumstances in a light-thermostat (HORVÁTH and LASZTITY, 1965), the incipient flowers of broad-bean were treated with colchicine to supplement the seed-treatment. The experiments were repeated 3—4 times, and on every occasion the chromosomes were examined with carmine-acetic acid staining on fresh preparations.

Results and discussion

In both concentrations applied the 1-hour colchicine treatment gave rise to polyploidy in broad-bean *(Vicia faba)* seeds. This is presented in the following photograph.

As regards the colchicine concentration and the age of the seedlings, no limits could be distinguished for the appearance of the polyploid cells. The effect of colchicine was manifested even when polyploidy had not yet appeared. The mitotic



Tetraploid root meristem cell of *Vicia faba*

cycle was retarded, as shown by the relatively large number of cells to be found in the prophase as compared with the control. Study of the mitotic phases did not lead to a result (see Table). After 1-hour colchicine treatment at a similar concentration in onion *(Allium cepa)*, the percentage mitosis increased in comparison to the control, the mitosis of the root-tip meristem cells being stimulated. Every division

Study of cell division on samples taken from the division zone of rootlets of colchicine-treated *Allium cepa* and *Vicia faba*

Variants	Colchicine concn. mg/100 ml	Treatment time min	No. of cells	No. of dividing cells	% Division	Phase distribution of dividing cells			
						Prophase	Metaphase	Anaphase	Telophase
4-day Allium cepa	1	60	365	153	49.86	132	9	9	3
	5	60	337	149	45.73	141	6	2	0
	control	—	507	138	35.25	116	17	5	0
4-day Vicia faba	1	60	515	84	18.00	49	9	12	15
	5	60	297	77	27.70	49	15	6	6
	control	—	467	145	31.50	53	23	27	37

phase occured in greater number than in the control. In onion the colchicine treatment stimulated the course of the entire mitotic cycle. The effect depends not only on the concentration of the colchicine and the duration of the treatment, but also to a large extent on the species and age of the seedling (Table).

In onion, polyploid cells were observed after the 10-hour colchicine treatment, but not in the case of ethyl methanesulfonate treatment.

When colchicine-treated broad-bean seeds were grown to seed-bearing, the tetraploidy did not remain. Treatment of the incipient flowers was effective.

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STUDY OF REGENERATION IN PEARL BEAN AND SUNFLOWER SEEDLINGS

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Abstract

In experiments on root regeneration a study was made of the cell division, the variation in the amount of soluble protein, and the effects of β-indolylacetic acid and kinetin compared to the control.

In the course of the regeneration following the cutting-back of the rootlets of seedlings (Pearl bean, Iregi csikos sunflower) the amounts of soluble protein in the roots and shoots were higher than in the control, while the intensity of the cell division also developed similarly in the root meristem cells. Auxin and kinetin increased the amount of soluble protein in Pearl bean seedlings, and gave rise to inhibition in this period of the regeneration in sunflower seedlings.

Various inhibitors of protein synthesis also act on the division and elongation of the root cells (IVANOV, 1970). As a result of auxin treatment the root formation is accelerated and the elongation growth too is enhanced (DUBOUCHET, 1968; FELLENBERG, 1969). Indoleacetic acid treatment first increases, then decreases the growth, and later a second increase of rate ensues (TRUELSEN, 1966). Gibberellic acid inhibits regeneration (PREVOT, 1968). The regeneration of decapitated stem is inhibited by higher concentrations of kinetin (HILLMAN, 1970).

In our experiments on root regeneration a study has been made of the cell division, the variations in the amounts of soluble protein, and the effects of β-indolylacetic acid and kinetin compared to the control.

Materials and Methods

Experiments were carried out with white Pearl bean (Baranya county variety) and sunflower (Iregi csikos). Germination was performed on filter paper moistened with distilled water, in Petri dishes in a 23 °C thermostat. The reserve nutriment was used up for the growth of the seedlings and there was little nitrogen uptake from the once-distilled Szeged water.

In the first part of the experiments some of the 3-day seedlings were left as control, while the others were cut back to 1-3 of the rootlets. Regeneration of the rootlets began on the third day after the cutting-off. A study was made of the chromosomes and the development of the cell size in the meristem tissues of the regenerated and the control root apices by carmineacetic acid staining on fresh preparations. Subsequently the regenerated roots were again cut back and the division of the meristem cells of the root apices regenerated for a second time was compared with that for the once regenerated case and for the control.

In the second part of the experiments the variation of the total amount of soluble protein in the roots and shoots of the regenerated and control seedlings was examined as a function of the regeneration time. Some of the cut-back rootlets were treated with auxin, and others with kinetin. The two hormones were applied in a concentration of 1 mg/1000 ml deionized water. The total soluble protein was determined on the basis of the method of LOWRY et al. (1951).

Results and discussion

These experiments permit the conclusion that the regeneration initiates active processes of synthesis in the plants, thereby increasing the extent of the mitotic cell division and the growth associated with it. These results are summarized in Table 1.

Table 1. Variations in division and size of meritem cells in regenerated and control rootlets Sunflower Pearl bean

Variants	Regeneration time days	Once regenerated						Twice regenerated						Size of R cells as percentage of size of C cells	
		No. of cells studied		No. of cells dividing		Extent of division, %		No. of cells studied		No. of cells dividing		Extent of division, %		Length	Cross-section
		C	R	C	R	C	R	C	R	C	R	C	R		
Pearl bean	3	106	82	35	2	33.01	2.43	58	99	16	5	27.00	5.05	1.28	0.92
	5	56	192	18	66	32.14	36.26	72	40	21	25	29.16	62.50	1.25	0.60
	6	142	96	39	37	27.46	21.12	63	74	38	35	60.31	47.29	1.25	0.76
Sun-flower	3	188	175	103	32	54.78	18.20	153	238	73	187	47.70	51.80	0.71	0.63
	5	176	179	113	174	64.20	98.86	137	162	22	79	16.05	48.70	0.98	0.82
	6	198	157	161	114	81.31	72.61	50	22	7	2	14.00	9.00	0.10	0.90

Explanation of symbols: C = control
R = regenerated

It can be seen from the Table that the intensity of division of the regenerating rootlets exceeds that of the controls. The extent of division decreases with the progressing of the regeneration. The extent of the decrease may be brought about by the fact that there is a reduction of the synthesis processes, since the organ is regenerated and there is not sufficient nutriment for growth, and the elongation of the cells assumes prominence. The twice cut-back and again regenerating rootlets exhibit a more intensive division, but for a shorter time than when first regenerated. The

Table 2. Variation of the total amount of soluble protein in the rootlets and shoots as a function of the regeneration time. Calculation: mg/g fresh weight

Variants	Time from regeneration, days	Control		Regenerated		Auxin-treated		Kinetin-treated	
		Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
Sunflower	4	20.70	41.50	20.70	36.05	12.90	39.50	11.40	39.60
	5	13.80	35.55	22.20	36.75	17.30	40.90	18.50	39.80
	6	12.80	36.75	17.85	42.75	18.00	39.60	17.10	40.00
	7	14.50	25.50	18.50	33.45	18.80	27.50	17.90	33.90
	8	15.00	19.35	16.50	26.40	16.40	17.60	17.30	17.80
Pearl bean	4	19.50	40.35	23.55	33.60	22.65	39.15	25.35	31.80
	5	19.80	32.40	27.45	32.70	24.30	40.35	22.35	26.26
	6	17.55	32.70	17.85	24.90	23.85	35.20	18.15	24.15
	7	16.00	17.10	17.70	26.25	16.80	31.80	17.40	20.85
	8	15.15	18.45	15.75	16.80	18.60	33.15	18.30	12.00

size of the cells too is decreased in comparison to the control. In the second regeneration there is not a sufficient supply of ions to induce the turgor, and hence the elongation of the cell, which would be enlarged, does not take place. The minimum nutriment supply no longer exists, and accordingly the optimum plasm consistency of the cells can not develop.

Table 2 shows the change in the total amount of soluble protein in the rootlets and shoots of the regenerated and the control seedlings. The effects of auxin and kinetin on the regeneration are also presented here.

It can be seen that the total amount of soluble protein is greater in the regenerated roots and shoots, for because of the reformation of the organ the synthesis of proteins is more intensive than in the controls. The effects of auxin and kinetin on the regeneration are affected by the species, age and mode of treatment of the plant. This was also found in our experimental plants too. The two hormones affected the regeneration of the two plants in different ways. Our data show that both auxin and kinetin accelerated the regeneration in the rootlets of the Pearl bean, and stimulated the protein synthesis, for the amounts of soluble protein in the roots and the shoots are high. The concentration of kinetin employed inhibited the growth of the shoots of Pearl bean, and the amount of protein examined was concentrated in a smaller part.

In sunflower seedlings auxin and kinetin periodically inhibit and stimulate the regeneration of the rootlets, depending on the age of the seedlings. If the total amount of soluble protein rises above the value for the control in the course of the regeneration, both hormones act as inhibitors, whereas in other cases they give rise to stimulatory effects.

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VERSATILE AUTOMATIC COULOMBMETER

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Abstract

The apparatus is suitable for following reactions in which one of the reaction partners is a gas, the consumption of this being replaceable by electrolysis. The volume of gas reacted can be determined from the measured charge values. The equipment consists of a glass apparatus comprising an elctrolysis cell and the reaction vessel, which can be thermostated, together with the electrical unit and the magnetophone for the recording of the results: this permits rapid subsequent evaluation

By definition coulombmetry is a method whereby extremely small amounts of materials can be determined conveniently and quickly. The method has the very great advantage that the appropriate apparatus can readily be automated.

The method can also be used to advantage in biological and biochemical examinations; this will be exemplified below.

Since the measurement of the amount of charge can be traced back to the measurement of time, the electrodes must be connected to constant current. If modern electronic elements are utilized it is not difficult nowadays to construct supply sources of very high stability.

Apart from the coulombmeter reported in the present paper, attention is paid to the construction of an apparatus which functions continuously and possesses a closed regulation circuit. In this system the value of the current strength passing depends on the pressure, or on the difference in levels, which is proportional to the pressure. By the application of an appropriate correlation between the current strength and the difference in levels, it is possible to achieve very high accuracy and excellent dynamic properties.

However, the construction of such an apparatus is very expensive, and is justified only if it is necessary to follow rapid changes in a wide range.

We set out to construct an automathic instrument, which is easy to handle, contains the most modern elements and requires little space. The instrument is suitable for investigations in which one of the reactants is a gas.

Experimental technique and Methods

For homogeneous hydrogenation a coulombmeter was first used by Nagy and Simándi (1962), the stabilized supply source and recorder being prepared on the basis of the paper of Telcs and Nagy (1961).

Beck and Gimesi (1963) investigated the effect of F^- on the activation of molecular H_2. This work was repeated coulombmetrically by Beck and Gaál, an

the same activation enthalpy and entropy values were found, proving the reliability of the method.

The rate of reduction of Ag^+ was calculated by means of the relation given by NAGY and SIMÁNDI (1962):

$$W = f \cdot I_0 \cdot \operatorname{tg} \alpha$$

in which the value of f in the case of H_2 is 5.18×10^{-7} (solution volume in ml $0.5/96\,500 = 5.18 \times 10^{-7}$). The dimensions of the rate are mole/litre · sec. I_0 is the strength of the current measured in milliamperes. The value of $\operatorname{tg} \alpha$ is obtained by plotting the total time of electrolysis as a function of the reaction time and taking the quotient of the differences.

The apparatus works on the principle that when the solution reacts with the gas, then the pressure in the gas space above the solution decreases. As a result of the fall in pressure the liquid level rises in the arm of the electrolysis cell connected to the closed space, and in the other arm the liquid moves away from the Pt contact. Consequently, the relay connects constant current to the Pt electrodes.

The gas evolved equalizes the pressure and the cycle is repeated.

The apparatus of NAGY and SIMÁNDI (1962) has been modified in that the reaction vessel is connected via the stopper to the coulombmeter proper, so that it can be removed easily to facilitate cleaning (Fig. 1).

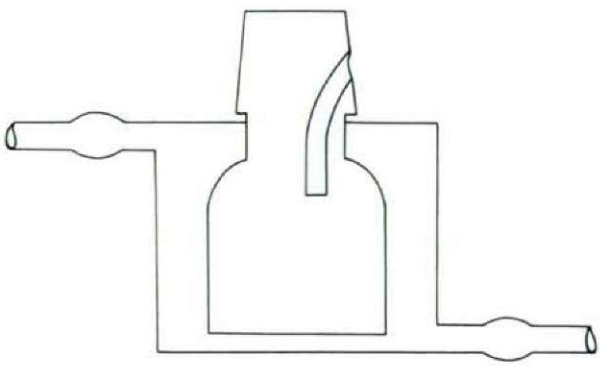

Fig. 1. Reaction vessel of glass apparatus, connected via stopper to the instrument.

The reaction mixture may be stirred with a magnetic stirrer.

The two electrodes are contained in vessel *b*, as shown in Fig. 2, there also being a Pt auxiliary electrode in that part open to the atmosphere; this serves for the development of the contact. The purpose of the U-tube in part *a* is to make the apparatus suitable for the measurement of the consumption of a gas reaction partner not prepared by electrolysis. A convenient sealing fluid is placed in the U-tube and the part leading to the reaction vessel is filled with the actual gas. The volume of the reaction space is 100 ml, only two-thirds of this generally being used.

In other cases this U-tube can also be used to effect the adsorption of carbon dioxide released in the course of the uptake of oxygen by biological materials.

If it is desired to measure the rate of the reaction on a non-linear section of the function, then the actual amount of oxygen can be calculated from the well-known formula

$$m = \frac{M}{n \cdot F} \cdot i \cdot t$$

where M is the formula weight, n the change in the number of electrons, F the Faraday number, i the current strength in amperes, and t the time in seconds.

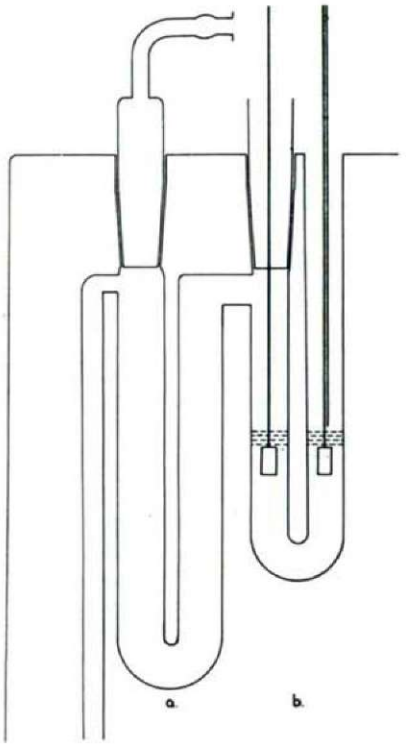

Fig. 2. a) sealing fluid in U-tube, b) the electrolysis cell with electrodes and contact.

Supply source

An outline of the integrated-circuit, stabilized supply source can be seen in Fig. 3.

The range of operation of the supply source is 0.5 mA—1 A, with a maximum output voltage of 15 V. The stability of the supply source is better than 0.1% ensured by a precision voltage-regulating integrated circuit (FAIRCHILD U6A7723393).

The current strength can be established by variation or switch-over of resistance R. The value of R may be determined from the approximate formula

$$R(\Omega) = \frac{7{,}15\ V}{I_{out}\ (A)}$$

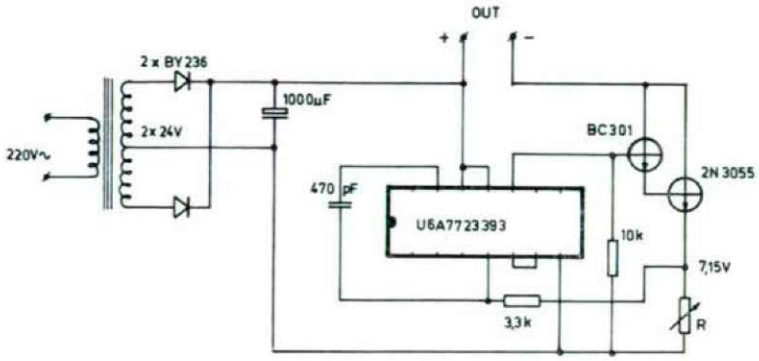

Fig. 3

To ensure the stability it is advisable to use stable resistances with low temperature coefficients.

Change in the liquid level in the electrolysis cell (Fig. 2b) is sensed via one of the electrolysis electrodes and an auxiliary electrode.

On the making of the contact, the 50 Hz alternating potential at the auxiliary electrode gives rise to a current only in the microampere range, and this causes no electrolysis. As mentioned above, however, when the circuit is closed the electrolysis ceases, for the amplified and rectified alternating current interrupts the electrolysis by switching out a relay.

The reaction time and the amount of charge used during the reaction are measured by counter relays. The time is measured in seconds. The counter relays are controlled by a 50-fold attenuation of the mains frequency, with the aid of digital integrated circuits. The first counter relay continuously measures time from the beginning until the end of the experiment. The other two relays in turn measure only the time of the electrolysis. Depending on the position of the switch, the switch-over can be made at 0.5, 1, 2, 4 or 8-minute intervals. The current strength can similarly be adjusted by switch, to 10, 20, 50, 100 or 200 mA. The experimental results can be comfortably read off the non-operating relay by suitable arrangement of the switch-over time.

For the acceleration of the evaluation in long-time experiments it is practical to automate the apparatus, i.e. to provide the possibility that the amounts of charge relating to the various time values be read off subsequently too.

The apparatus developed affords two possibilities for this: by connection to a recorder or to a magnetophone.

Recorder connection

The apparatus can be connected to a 10 mV recorder, by means of which the time of electrolysis can be recorded as a function of the reaction time.

When the current-stabilizer is switched on, the apparatus sends a 6—7 mV signal to the recorder, and this lasts until the time of switching off. The instrument produces a small mark on the recorder chart at previously determined time intervals, and this permits the exact reaction time to be established.

Magnetophone connection

Recording of the signal on a magnetophone seems to be the most convenient and accurate procedure. At the end of the reaction the result of the experiment can be played back at any desired time, at a rate much higher than the rate of recording. It is practical, therefore, to record at the lowest rate.

An M11 magnetophone was used. The gearings were arranged so as to give a quotient of the recording playing-back rated of 8. Thus, the subsequent playback is eight times shorter than the total reaction time.

The coulombmeter causes a short impulse to be recorded on the tape every second, while in addition to these impulses a 700 Hz A.C. signal is also recorded when the current-stabilizer is switched on.

When the magnetophone is played back it must be connected to the coulombmeter, which senses the signals recorded on the tape and accelerated eight times, and causes the counting relays to operate as in the recording.

The magnetophone need not be stopped during the playback, for as mentioned earlier the relays can be preset to switch over periodically, and there is always sufficient time to read off the value from the non-operating relay.

Sources of error

1. Variation of the temperature can give rise to a considerable change in the pressure of the gas in the reaction space, and it is therefore essential to maintain the temperature constant.

2. The change in the course of the electrolysis of the volume of the electrolyte solution is negligible, for the few ml of gas evolved correspond to only a very small volume of liquid.

3. Pressure correction. In measurements lasting for a long time a barometer correction must be made if the atmosheric pressure changes appreciably meanwhile. Increase of the air pressure results in an increased time of electrolysis and this causes a positive error.

If the volume of oxygen resulting from the change in the external air pressure is $V(t)$, the volume of the reaction space is V_0, the initial atmospheric pressure is P_0, and that at time t is $P(t)$, then

$$V(t) = \frac{P(t) - P_0}{P_0} \cdot V_0.$$

If the volume of gas taken up is plotted as a function of time, the actual volume (V_{act}) is the difference of the measured volume and $V(t)$.

Use of the apparatus

The apparatus can be employed to measure the oxygen-uptakes of plant and animal tissues. As plant material barley was grown to the age of 10 days, and the shoots then homogenized in phosphate buffer of pH 6. The results are illustrated in Fig. 4.

For material of animal origin the apparatus was used to study the the oxygen-uptake of snail heart. The snail heart was placed in Ringer solution as reported by RIPPLINGER and HEROLD (1970). The experimental results are shown in Fig. 5.

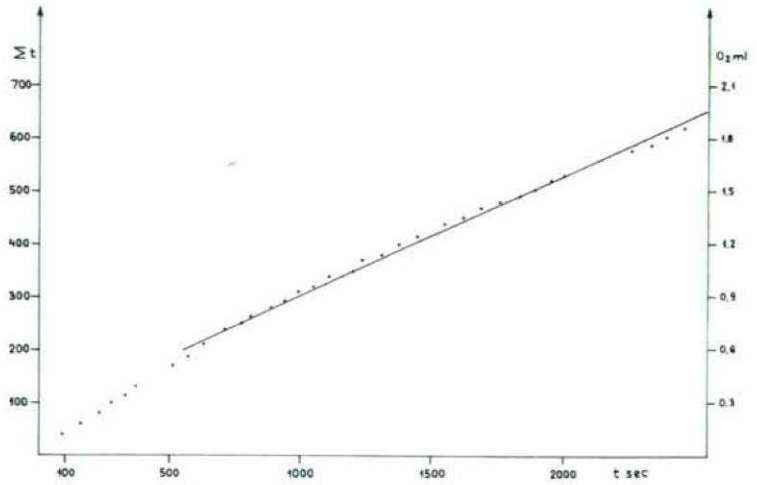

Fig. 4. Oxygen-uptake of barley homogenizate in phosphate buffer of pH 6 at 29 °C. $I_o = 50$ mA.

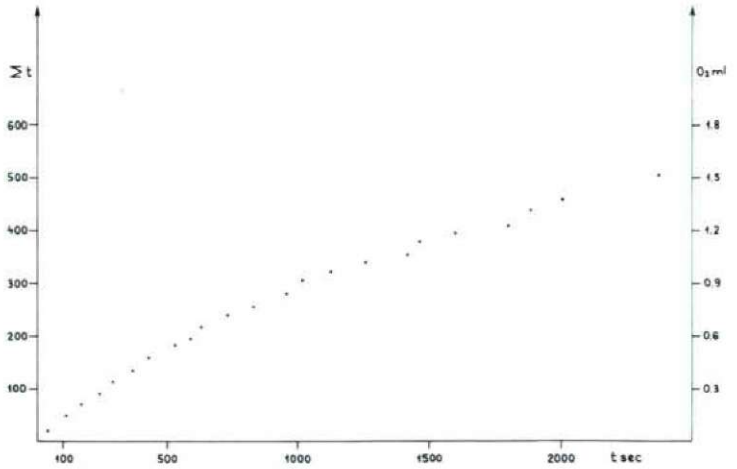

Fig. 5. Oxigen-uptake of smail heart at 29 °C. $I_o = 50$ mA.

Among many other possibilities, the method is excellently suited to the following of enzymatic hydroxylation with molecular oxygen (6).

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DATA ON THE EPITHELIAL CELLS OF THE TRACHEAL GILL EPHEMEROPTERA: PALINGENIA LANGICAUDA OLIV.

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Abstract

The filamental epithelial cells of the gill plate of the larvae are poor in organelles, and a plate-system is to be found on their surface. The epithelial cells of the gill plate are richer in organelles, and produce cuticula and characteristic dense granules.

Investigation of the histological structure of the tracheal gill of *Palingenia longicauda* OLIV. led earlier to the description of some modified epithelial cells which are involved in the structure of the campaniform sensillae (CSOKNYA and HALÁSZ, 1972). If the gills of larvae in different states of development are examined, further modifications of the epithelial cells can be observed. The aim of the present paper is to describe these.

Materials and Methods

The studies were carried out on the tracheal gill of *Palingenia longicauda* OLIV. (Ephemeroptera). The gill plates were fixed in Palade osmium tetroxide (pH 7.4). For pusposes of electronmicroscopic examinations, after dehydration with alcohol and embedding in araldite the sections were contrasted with REYNOLDS' (1963) lead citrate. Photographs were prepared with Tesla BS 242 D and JEM 100 B electronmicroscopes.

For purposes of light-microscopic observations, 5—7-micron sections were prepared from material fixed in 10% formalin, which were subjected to haematein-eosin and van Gieson and Best carmine staining.

Results and discussion

The entire surface of the gill plate is covered by cover and epithelial cells, closely interconnected into one layer. Cuticula of various thickness can be seen on these cells (EASTHAM, 1936; WICHARD and KOMNICK, 1971; CSOKNYA and HALÁSZ, 1973), which as regards appearance and structure is not uniform over the entire area of the gill. On the unstructured plated there are connected layers with strongly dense surfaces, which alternate dark and light in the deeper parts; at high magnification, fibrillary structures can be observed in these layers. Within a layer these fibrils are arranged parallel to one another, curved in the form of a parabola. This agrees with the cuticula structure of other Insecta, the similarity being particularly striking in the region of the common integument. In the case of ephemera larvae, besides the fibrils electron-dense granules sometimes 600—1000 Å in diameter can also be observd (Figs. 3, 5 and 6).

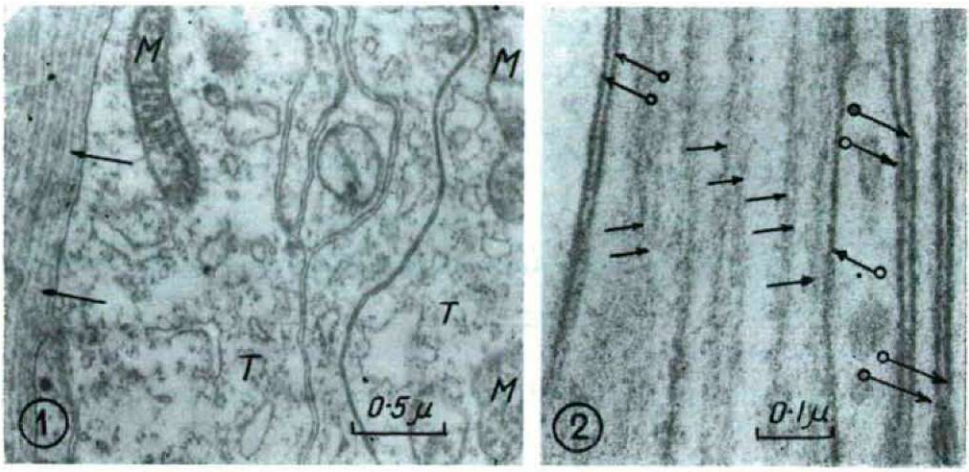

Fig. 1. Detail of epithelial cells of filament on electronmicroscopic photograph. There are many free ribosomes (T) in the cytoplasm. A multi-layered plate series (arrows) can be observed on the surface of the epithelial cell. M-mitochondrium.

Fig. 2. The structure of the plates (arrows) covering the surface of the filaments differs from the unit-membrane (arrows with circle) structure of the processes of the epithelial cells.

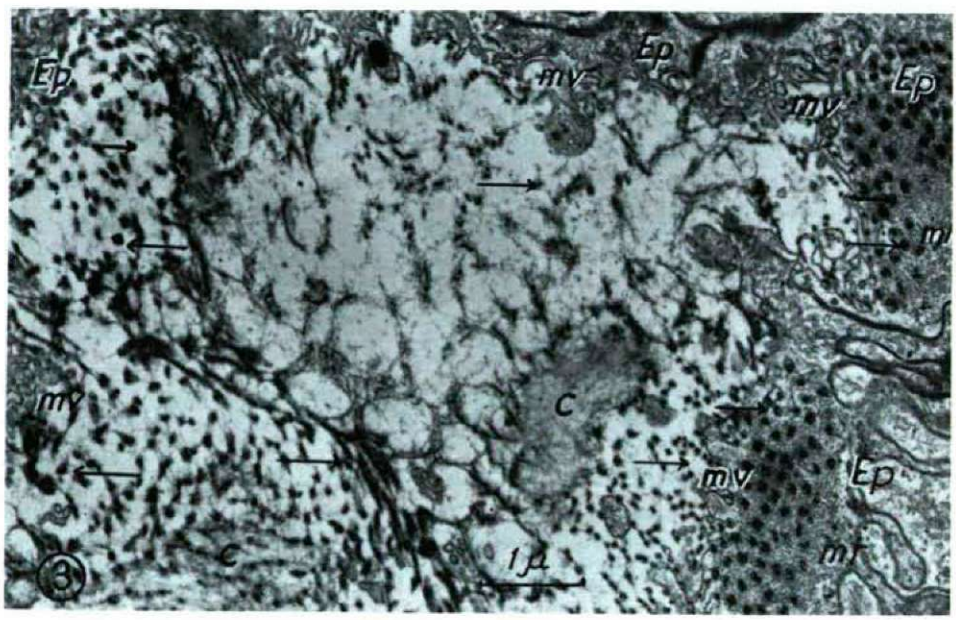

Fig. 3. Section parallel to the cuticula (c), with epithelial cells (Ep) of the unstructured section of the gill plate and with products. The surface of the cells is structured by microvilli (mv). The cells contain many microtubules (mt) and dense granules, which are incorporated into the cuticula (arrows).

On light-microscopic sections a thin, homogeneous border is visible on the surface of the epithelial cells of the filaments; this is the continuation of the previous cuticula, and gives the same staining as that. On electronmicroscopic photographs, however, it is clear that the structures of the two are different. Here it is a matter of a series of plates layered loosely on one another, which run parallel to the surface and thereby cover the epithelial cells. High-resolution photographs clearly reveal that the structure of the individual plates can not be identified with that of the well-known unit-membranes (Figs. 1 and 2). The thickness of the plates was found to be 40—50 Å, and their distance from each other about 50—350 Å. It is only very rarely possible to observe an (inner) plate adjacent to the surface of the cell, but at a greater distance from the epithelial cell; this may indicate that this system is more closely connected to the epithelial cells than is the cuticula. For instance, even in the periods between the moultings extensive interstices can frequently be observed between the cuticula and the underlying epithelial cells (Figs. 3 and 4). The surface of the epithelial cells too is different: below the plate series the epithelial cells have smooth surfaces (Fig. 1), whereas below the cuticula it is practically always possible to observe microvilli, which structure the cell surface (Figs. 3 and 5). It must be noted here that these plates can also be seen around the nerve bundles of the tracheal gill, as reported previously (CSOKNYA and HALÁSZ, 1972). The oxygen necessary for respiration presumably reaches the intercellular space and the haemolymph via the plate-system, with its different structure from that of the cuticula. On moulting the larvae lose this plate-system, similarly to the cuticula covering the body.

In spite of their considerable similarity, the epithelial cells of the gill plate, which give rise to the above-mentioned structures observed on their surface, also exhibit appreciable differences. This is due in part to the different abundances of organelles, and in part to their diversity. In addition to sporadic cisternae of the granulated endoplasmatic reticulum and some mitochondria, only free ribosomes occur in significant amount in the epithelial cells of the filaments. In contrast, the epithelial cells producing the cuticula contain large quantities of glycogen (Fig. 4) and many mitochondria in their deeper processes. Towards their surface, their microtubular substance increases strongly, among which vesicles 1000—1800 Å in diameter, possessing a dense content, appear close to the apical surface of the cell. As they approach the surface of the cell, their diameter increases, and then on the surface they open out to result in the very strong structuring of the surface (Figs. 3 and 4).

Moving away from the surface of the cell across the subcuticular interstice (Fig. 3), the dense material of the vesicles is deposited into the newly forming cuticula, and can be detected in it (Figs. 5 and 6). Study of many publications referring to the structure of the cuticula (SMITH, 1968; GNATZY and SCHMIDT, 1971; MORAN, 1971; MORAN, CHAPMAN and ELLIS, 1971; SCHMIDT and GNATZY, 1971) and of the high-resolution photographs presented in these, failed to reveal a similar phenomenon. Dense granules can be perceived in the cuticula in the photographs prepared by WICHARD, KOMNICK and ABEL (1972) on the chloride cells and cell-groups of the gill of certain Ephemeroptera larvae, but the authors make no mention at all as to the origin and function of these.

However, the surface cuticula in the region of the gill plate is produced not only by the above-mentioned cover cells, but also (in addition to their other functions) by the supporting cells of the campaniform sensillae, the trichogen and tormogen cells. It is assumed (SMITH, 1968; BLANEY, CHAPMAN and COOK, 1971; DALLAY,

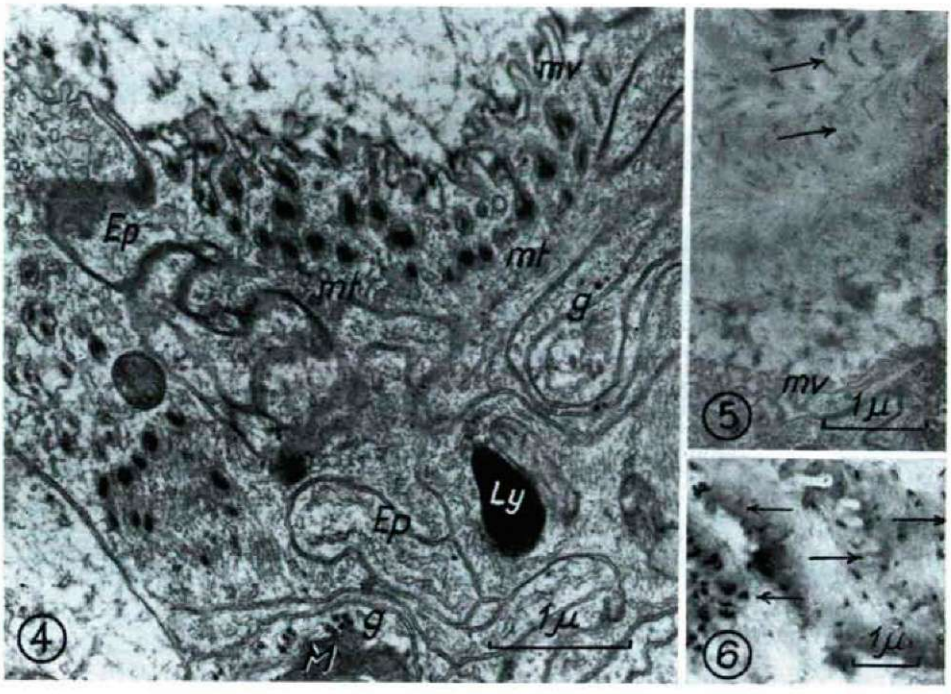

Fig. 4. Section (perpendicular to the surface) of processes of an epithelial cell (Ep) below the cuticula. The cell surface is made uneven by the microvilli (mv) around the discharging dense material. More deeply, glycogen (g) can be observed. M — mitochondrium; Ly — lysosome; mt — microtubule.

Figs. 5 and 6. The incorporated dense product (arrows) can be well seen between the regularly arranged cuticular ridges. mv — microvilli.

1971; GNATZY and SCHMIDT, 1971; SCHMIDT and GNATZY, 1971) that of these two types of cells it is the trichogen cells which produce cuticula more actively. These cells presumably take part in the formation of the microtubular bodies of the sensillae and of the exocuticular layer covering this, and in their reproduction after moulting (MORAN, 1971).

The cuticula production of the tormogen cells is less than that of the former cells; one should think here rather of the formation of the extracellular fluid, which collects in the extracellular cavity around the sensory process (SMITH, 1968; GNATZY and SCHMIDT, 1971; MORAN, CHAPMAN and ELLIS, 1971; SCHMIDT and GNATZY, 1971).

Comparison of the trichogen and tomogen cells of ephemera larvae does not reveal characteristics in their structures which might be used to explain the fundamental and essential functional differences.

The young Insectae are known to moult several times, as the old cuticula impedes their growth. This moulting is assisted by the moulting fluid (SMITH, 1968; BLANEY, CHAPMAN and COOK, 1971; GNATZY and SCHMIDT, 1971; MORAN, 1971; SCHMIDT and GNATZY 1971), which progressively raises the old cuticula, collecting in the space between the epithelial cells and the cuticula. In the case of the ephemera

larvae we were unable to distinguish characteristic cells or cell-groups which produce this moulting fluid, and thus we must assume that this too is a function of the epithelial cells.

Acknowledgments

The authors wish to express their thanks to Prof. FERENC GUBA, Director of the Department of Biochemistry, University Medical School, Szeged, for permission to use the JEM 100 B electron-microscope, and to ROZÁLIA VINCZE and ERZSÉBET SZÉLL for expert technical assistance in the preparation of the sections.

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ZOOBENTHIC STUDIES ON THE LOWER REACHES OF THE TISZA AND MAROS

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Abstract

Zoobenthic investigations were carried out in 1963—64 in the lower reaches (Szeged environment) of the rivers Tisza and Maros. The results of the collections led to the following conclusions:

1. The bottom fauna of the lower reaches of the Tisza is richer than that of the Maros both qualitatively and quantitatively.
2. Substantially fewer animals live on the bottom in the middle of the river beds than near the banks. The proportions of the zoobenthos found near the banks were 74% and 60% in the Tisza and Maros, respectively.
3. The dominant taxonomic group in the Tisza was the Oligochaeta, and in the Maros the Diptera (Chironomidae).
4. The richest bottom zoocoenoses of the rivers were the lithorheophil and pelorheophil.
5. The quantitative distribution of the zoobenthos was affected decisively by the fluctuation of the water-levels of the rivers and by the nature of the bottom.
6. The frequency of the common occurrence of the Oligochaeta + Diptera (Chironomidae) was characteristic in these two rivers.

Introduction

The author began a zoobenthic study of the Tisza and the Maros in 1963. Up to that time there had been no systematic research of a similar nature into these two Hungarian rivers. Since that date the author has been investigating the macrobenthos of the two rivers as a member of the Tisza Research Group.

The Tisza, the largest tributary of the Danube, flows through the most deeply sunken region of the Great Hungarian Plain, absorbing practically every watercourse in the eastern half of the Carpathian basin. Its length is 977 km, its catchment area in all 157,186 km², and its average rate of flow at Szeged 786 m³/sec. Its water level tends to extremes: its depth and range of floods are the greatest in the lower reaches. Flood-waves appear from March and April until May—June.

The largest left-hand tributary of the Tisza is the Maros. Its length is 880 km, its catchment area 27,049 km². It runs into the Tisza at Szeged with an appreciable drop (27 cm/km), depositing alluvium consisting of much medium and coarse sand into the slow water of the Tisza (a drop of 3 cm/km, with an alluvium mainly of fine mud) below its mouth.

The waters of the Tisza and Maros have the same calcium hydrocarbonate features, but the sodium, sulphate and chloride contents in the Maros at times and in certain places attain significant values. The oxygen consumption of the water of the Maros is more than 25 mg/l and thus, with the exception of the short section

at the mouth, is more polluted than the a—*b* mesosaprob Tisza water. This latter is yellowish-grey from the much agitated, fine alluvium, its transparency varying in the range 25—200 mm (average value 90 mm).

During the investigation period the pH of the Tisza water was 6.7—8.1, and that of the Maros 6.2—6.4.

Methods

The bottom samples were taken with a modified Petersen sampler (dredging area: 800 cm^2); the material was washed with a 0.28 mm mesh metal sieve, sorted by hand, and preserved in 6% formalin. The species were determined on non-fresh material.

Collecting sites

Mud samples were collected from the lower reaches of the Tisza (Szeged environment) from June, 1963 to July, 1964, on all occasions in the vicinity of the two banks (ca. 5—6 m from the bank) and from the middle of the bed, i.e. 3 samples per collecting site. The three collecting sites were 3 km apart (Fig. 1).

Collecting site I: Directly below the Szeged Ship-Repair Yard. The right bank is rich in detritus, and thick, soft mud. Water-depth: 0.5—4 m (at high water 6.6 m). The left bank is muddy clay; the water-depth during the collecting period was 0.5—4 m. At the middle of the bed the bottom is sand, with a little mud, and the water-depth is 5—6 m (of the 12 sampling sites, this one had the deepest water).

Collecting site II: 3 river km lower. The right bank is muddy, its water-depth 0.5—4 m; the left bank is muddy sand, its depth 0.5—3 m (at high water 7 m). Here too the middle of the bed is sandy, its depth 2—3 m (max. 5 m).

Collecting site III: A further 3 river km lower. The right bank is stony mud, its depth 0.5—4 m; the left bank is clayey, and in general only 0.5 m deep (at high water 6—8 m).

Simultaneously with the collections from the Tisza, bottom samples were also taken from the Maros, 300 m from the mouth. In the vicinity of the right bank the bottom is muddy sand, its depth 0.5—3 m (max. 9 m). The left-bank samples came from a muddy bottom, where the water-depth was 0.5—1.5 m (max. 9 m). Here too, similarly to the Tisza, the middle of the bed is sandy, and the water generally 1—2 m deep (max. 10 m).

Results

In the material from 101 samplings on altogether 9 occasions (monthly, excepting the winter months), a total of 8964 animals were found.

In the evaluation of the collection results, an answer was sought to the following questions:

1. Is there any difference in the zoobenthic fauna of the lower reaches of the two rivers?
2. What are the differences between the bank-side and central-bed zoocoenosis parts of the rivers?
3. What are the characteristics of the zoocoenoses of the individual bottom types (sandy, muddy, clayey, etc.)?
4. What are the relations to each other of the more important taxonomic groups, and their quantitative distribution?
5. What is the trend of the population dynamics of the more frequent and more typical Oligochaeta species?

From the examination results it can clearly be stated that the zoobenthic fauna of the Tisza is the richer both qualitatively and quantitatively: in 75 samples the total number of individuals was 7875; the average number of individuals per sample was 105, and they represented 13 taxonomic groups. The bottom fauna of the Maros exhibits a poorer composition as regards quality and quantity: in 26 samples there were 1089 individuals, with an average 42 individuals per sample, and 9 taxonomic groups.

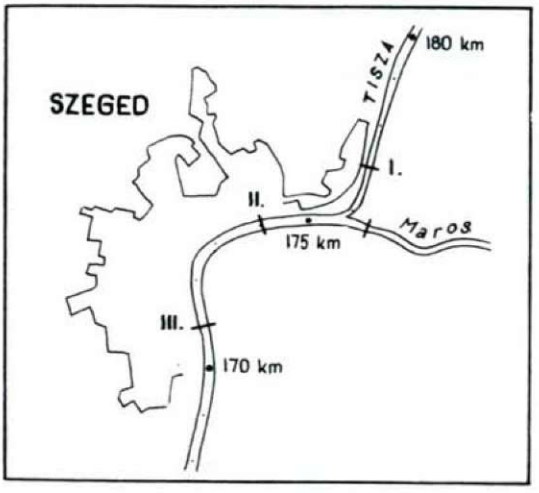

Fig. 1. Collecting sites in the lower reaches of the Tisza and Maros.

The dominant taxonomic group of the bottom fauna of the Tisza is the Oligochaeta, but the Diptera and Mollusca, as the other two groups with major numbers of individuals, also achieve relatively high dominance values. In the Maros, on the other hand, the Diptera is the dominant taxonomic group, showing a very strong predominance compared to the other two (Fig. 2). In the evaluation of these data, however, it should not be forgotten that the material being compared was not obtained from equal numbers of samples.

The zoobenthic fauna of the middle of the bed was the poorest for both rivers:

Tisza: average no. of individuals per sample: 50.25

Maros: average no. of individuals per sample: 32.43.

The richness in individuals of the part-side biotopes was greater:

Tisza: right-bank ave. no. of ind. per sample: 168.71
left-bank ave. no. of ind. per sample: 117.30

Maros: right-bank ave. no. of ind. per sample: 63.33
left-bank ave. no. of ind. per sample: 32.78.

When the individual collecting sites were studied separately as to the nature of their bottom, the zoocoenosis part types could be characterized as follows (Fig. 3):

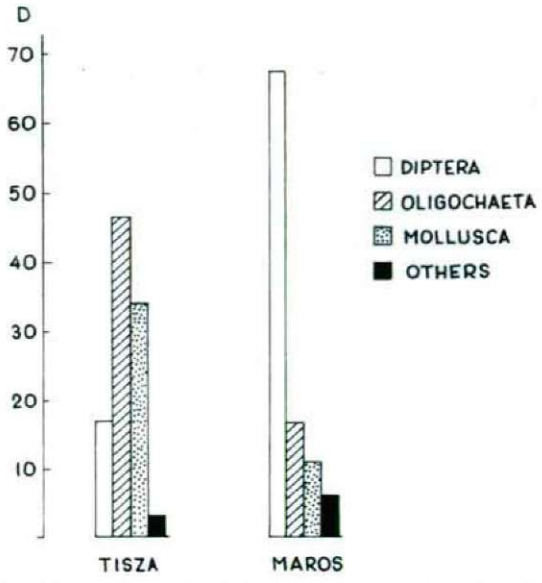

Fig. 2. Percentage distribution of the more important taxonomic groups of the zoobenthos in the lower reaches of the Tisza and Maros.

Lithorheophil: Tisza collecting site III, right-bank, where there are varied stones on the muddy bottom. This is the richest zoocoenosis (2885 individuals per m^2), and the only one where the Mollusca dominance is maximum. The majority of the Mollusca were *Lithoglyphus naticoides*. The Oligochaeta, which generally occur in the highest individual numbers in other sites in the Tisza, here comprise the lowest percentage of the zoocoenosis; typical species are *Tubifex tubifex* and *Limnodrilus* genus. The Diptera similarly lived in low individual numbers in this site.

Pelorheophil: Tisza collecting sites I and II, right-bank, and Maros left-bank; the second richest zoocoenosis (1851 and 415 individuals per m^2). A bottom type rich in organic detritus, its fauna being primarily characterized in the Tisza by maximum Oligochaeata dominance. Those occurring in high individual numbers were mainly *Limnodrilus udekemianus, Limnodrilus michaelseni* and *Isochaetides newaensis. Limnodrilus udekemianus* finds its optimum living conditions on the muddy, detritus-rich bottom, both in standing and in flowing water, and in such places it is to be discovered in high individual numbers.

Argillorheophil: Tisza collecting sites I and III, left-bank. As regards the quantitative richness of the zoobenthos, this zoocoenosis part stands in third place (1503 individuals per m^2). The leading species of Oligochaeta here is *Branchiura sowerbyi*, with *Limnodrilus michaelseni*.

Psammopelorheophil: Tisza collecting site II, left bank, where the average individual number of the zoobenthos is 1387 per m^2; also the Maros right-bank collecting site, which as regards density of individuals was the richest Maros site (63 individuals per m^2). The most frequent Oligochaeta species: *Limnodrilus claparedeanus* (in the Tisza) and *Limnodrilus hoffmeisteri* (in the Maros). This latter species generally occurs typically on sandy-muddy bottoms.

Psammorheophil: Characteristic everywhere in the middle of the beds of the Tisza and the Maros, and the poorest coenosis (598 and 350 individuals per m^2). Characteristic is *Isochaetides newaensis,* and relatively many *Naidida* species. The former species is commonly known to be frequent on sandy river bottoms. For this coenosis type the dominance of the Diptera taxonomic group instead of Oligochaeta is typical in general.

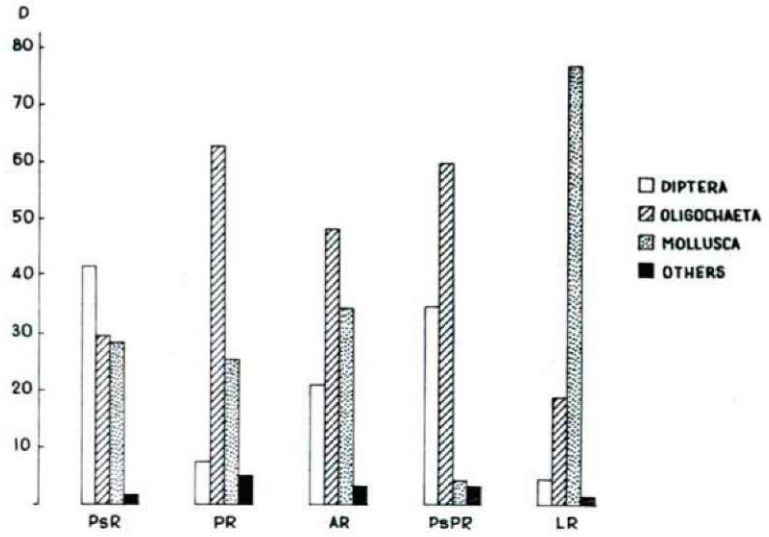

Fig. 3. Percentage distributions of the main zoobenthic taxonomic groups in the two rivers, according to bottom type.
PsR = psammorheophil
PR = pelorheophil
AR = argillorheophil
PsPR = psammopelorheophil
LR = lithorheophil

From a study of the relative percentage distributions (complex dominance) of the more populous taxonomic groups (Oligochaeta, Diptera, Mollusca) and the other groups with lower numbers of individuals ("other"), it can be stated that although there are differences in the individual collecting sites (Fig. 4) in the majority of the individual zoocoenosis types and in the whole of the Tisza reach examined the dominant group of the zoobenthos is the Oligochaeta. For all three collecting sites of the Maros, on the other hand, Diptera dominance is characteristic.

The question arises of what the observations in connection with the mosaic-complex composition of the zoobenthos of the rivers tell us about which are the groups whose members are most closely related, or in other words which occur most frequently together. From the study of the frequency of common occurrence (Agrell index) of the three taxonomic groups which are the most populous and most characteristic of the river reaches under investigation (Oligochaeta,Diptera, Mollusca), with regard to the individual zoocoenoses and the various river reaches, it can be concluded that the frequent joint occurrence of Oligochaeta + Diptera is characteristic of both the Tisza and the Maros:

Zoocoenoses	Ol+D	D+M	Ol+M
Psammopelorheophil	83	40	40
Argillorheophil	83	60	61
Pelorheophil	67	41	52
Lithorheophil	83	67	83
Psammorheophil	59	68	46
Tisza lower reach	76	62	66
Maros lower reach	60	20	12
Tisza central reach	46	23	42

The explanation of this may well be a generally typical mode of nutrition for the species of these two groups. While the predominantly detritophage Chironomida species feed on plant and animal detritus on the surface of the mud, the Annelida eat the thicker layer of mud and the very finely broken detritus, and probably the animal droppings too. In this way they practically complement each other, and are dependent on one another, and this may explain the frequency of their common occurrence.

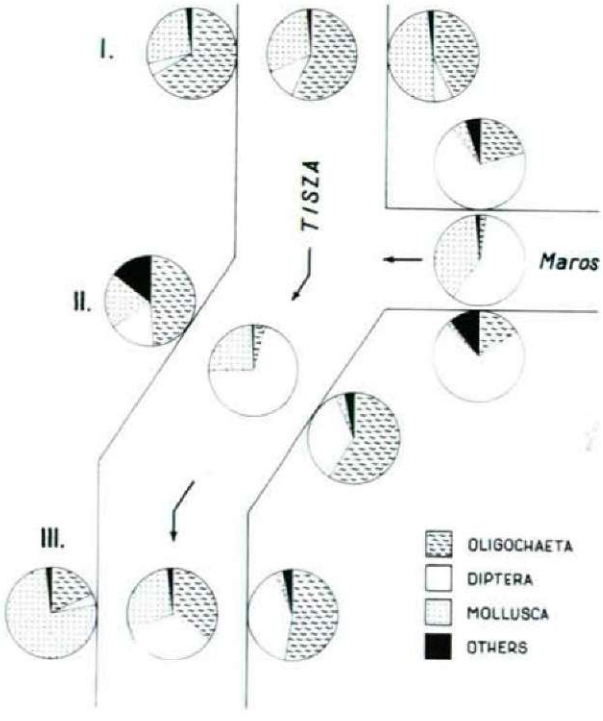

Fig. 4. Percentage distribution of the zoobenthic taxonomic groups in the sampling sites on the Tisza and Maros.

The fact that the Oligochaeta is the dominant taxonomic group in the zoobenthos of the rivers has a dual significance. As a result of their manner of feeding, they contribute greatly to the breakdown of the bottom-mud, promoting the functioning of the bacteria and hence the self-cleaning of the waters. Further, in their large numbers they serve as the most utilizable fish nutriment: their biomass in the Tisza is 3.64 g/m², and in the Maros 1.06 g/m².

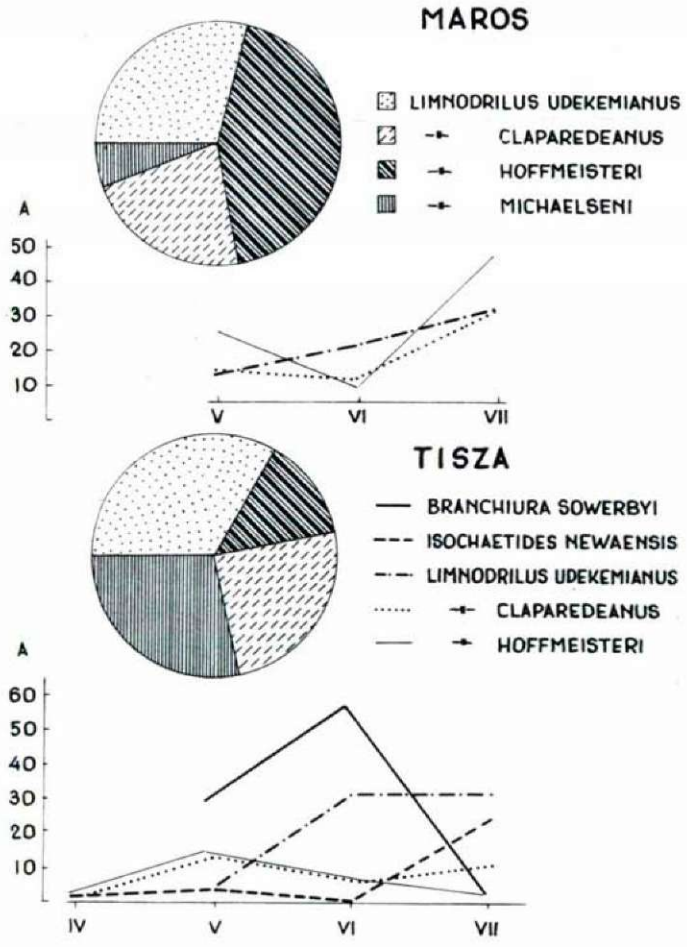

Fig. 5. Percentage distribution and population dynamics of more common Oligochaeta species of the Tisza and Maros.

The qualitative composition of the Oligochaeta is more varied in the Tisza (Fig. 5): here 15 species and taxons live, among which *Branchiura sowerbyi* is dominant, and *Isochaetides newaensis* condominant. Otherwise, about half of the Oligochaeta belong to the *Limnodrilus* genus. The most frequent of the eight species found in the Maros is *Limnodrilus hoffmeisteri, Branchiura sowerbyi,* one of the

largest fresh-water Tubificida, has visibly taken possession of the fresh-waters of Europe too. The author has found it in major amounts in the backwaters of the Tisza, and in the basins of fish lakes too (Fish-Production Research Institute, Szarvas). Because of its large size and frequency, it may play an important role in the nutrition of the fish-stock of natural Hungarian waters. *Isochaetides newaensis* is one of the characteristic species of sandy-muddy river beds. Its occurrence to date is known from Europe, and mainly from the area of the Soviet Union. *Limnodrilus hoffmeisteri* is to be found in smaller individual numbers in every biotope type, mainly favouring sandy bottoms. Its high dominance value in the Maros can probably

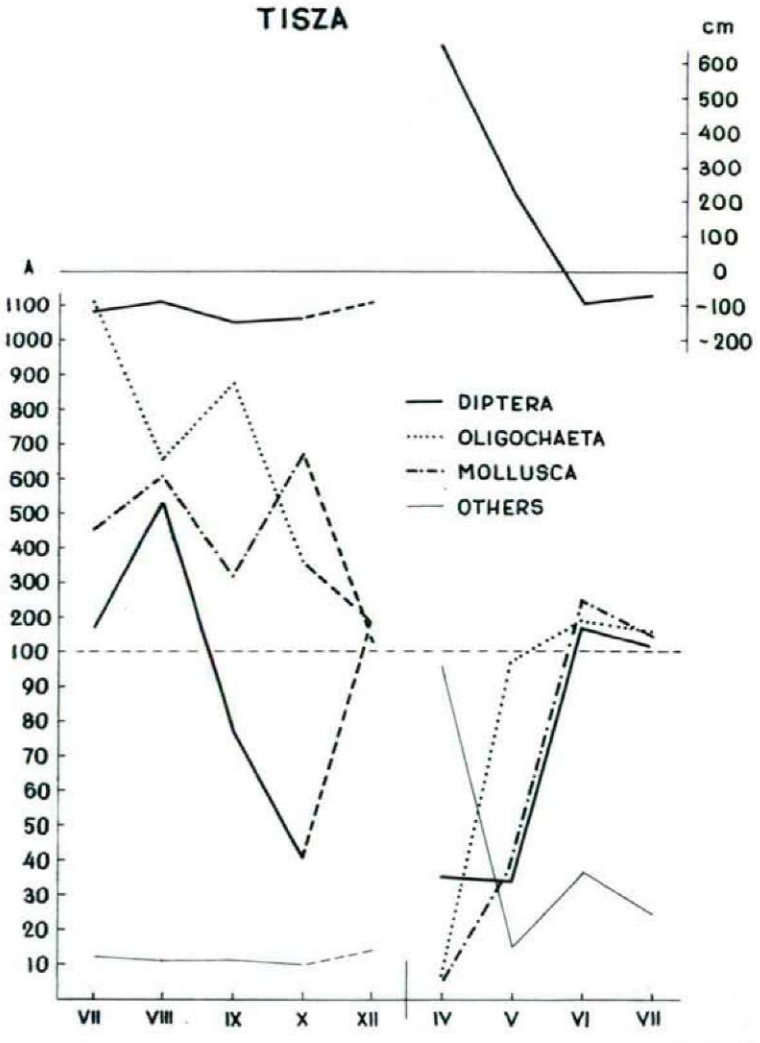

Fig. 6. Population dynamics and connection with the fluctuation of the water level of the Tisza for zoobenthic taxonomic groups.

be explained in that the endurance of this species to the chloride content of the water is considerable.

In the period studied the seasonal quantitative change of the Annelida is fairly great. The maximum is in July, when the new generation (cocoons and juvenile individuals) appears. This is naturally accompanied by a decrease of the prevailing biomass.

The change in the number of Annelida individuals is strongly affected by the fluctuation in the river water level (Figs. 6—7); the number of individuals exhibits a decrease or increase practically parallel to the rising or falling, respectively, of the water level.

88% of the Diptera taxonomic group was Chironomida. The maximum number of individuals could be observed in both rivers in August, this certainly being related to the time of swarming.

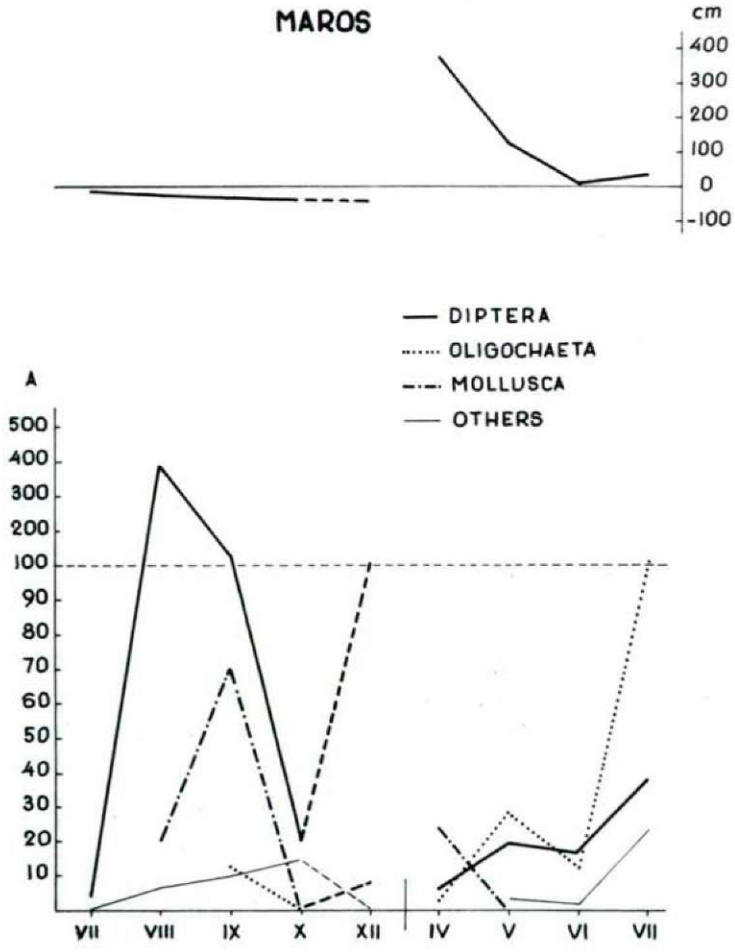

Fig. 7. Population dynamics and connection with the fluctuation of the water level of the Maros for zoobenthic taxonomic groups.

The Mollusca group was mainly represented by the snails *(Lithoglyphus naticoides!)*. The maximum of their dominance coincides with the autumn low-water state (September—October), when too following the rising water more animals collect on the same area.

The other ten taxonomic groups comprise only a small proportion of the zoobenthos of the two rivers. Their greatest dominance value was exhibited at high-water in the Tisza, the numbers of individuals of the Trichoptera and Amphipoda then increasing abnormally.

In the lower reaches of the two Hungarian rivers examined, practically half (43%) of the fauna of the zoobenthos was given by the worms, and mainly by species of the Tubificidae family (Fig. 8). The proportion of Mollusca was somewhat less (31%) (93% Gastropoda). The Diptera larvae and pupae (23%) comprise the main representatives of the Chironomidae family. The other arthropodal groups (Ephemeroptera, Odonata, Trichoptera, Coleoptera) make up 2% of the entire zoobenthos. In both rivers the Trichoptera may-flies and larvae can be found in relatively higher proportions (Tisza: 1.4%, Maros: 2.9%). A still more negligible constituent element of the zoobenthos is the Crustacea (1%).

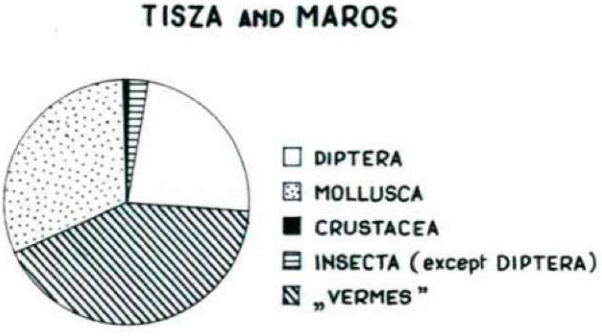

Fig. 8. Percentage distribution of the main zoobenthic taxonomic groups in the lower reaches of the Tisza and Maros (based on combined data).

They cannot be counted with essentially for the zoobenthos, but it was possible to find systematically colony-parts of Hydrozoa, Kamptozoa and Bryozoa species in various amounts on the bottom, in the form of detritus and mainly on Mollusca shells.

From the above proportions (without striving to attain generalities, which would be unsoundly based in the absence of an exact knowledge of the details), it can be concluded that detritophage animals are predominant in the macrofauna on the bottoms of the two rivers. The bottoms of the lower reaches of the rivers are mainly muddy, and generally rich in organic detritus. Such types of habitat are primarily suitable for the worms, molluscs and mosquito larvae in the main, as regards their feeding.

Zoobenthic species list for the lower reaches of the Tisza and the Maros (frequency notation: few –
medium +
many ○
mass ●).

Cnidaria, Hydrozoa
Cordylophora caspia –

Kamptozoa
Urnatella gracilis ○

Annelida, Polychaeta
Hypania invalida –

Oligochaeta
Limnodrilus claparedeanus ○
Limnodrilus michaelseni ○
Limnodrilus udekemianus ●
Limnodrilus helveticus +
Limnodrilus hoffmeisteri ○
Euilyodrilus danubialis +
Euilydrilus moldaviensis –
Euilydrilus hammoniensis –
Tubifex tubifex +
Psammoryctes moravicus –
Isochaetides newaensis ○
Branchyura sowerbyi ○
Criodrilus lacuum –

Hirudinoidea
Helobdella stagnalis –

Mollusca, Gastropoda
Lithoglyphus naticoides ●
Unio crassus +
Unio pictorum –
Dreissena polymorpha +

Tentaculata, Bryozoa
Paludicella articulata –
Plumatella repens +
Plumatella fungosa –
Plumatella fruticosa –
Plumatella emarginata –

Arthropoda, Isopoda
Asellus aquaticus –

Amphipoda
Dicerogammarus haematobaphes –

Gammarus pulex +
Corophium curvispinum +

Phyllopoda

Lepthesterias dahalacensis –

Ephemeroptera

Palingenia longicauda +
Caenis macrura –

Odonata

Gomphus pulchellus +

Trichoptera

Oecetis lacustris –
Orthotrichia tetensii –
Hydropsyche pellucidula ○
Hydropsyche ornatula –
Hydropsyche angustipennis +
Neureclipsis bimaculata –
Tinodes unicolor –
Limnophilus bipunctatus –

Diptera

Culicoides nubeculosus +
Dasyhelea versicolor –
Dasyhelea coarctata –
Chaoborus plumicornis –
Eukiefferiella similis –
Chironomus polytomus +
Chironomus gregarius –
Chironomus flavus ○
Chironomus chlorolobus –
Chironomus rostratus +
Chironomus camptolabis +
Chironomus tenuicaudatus -
Tanytarsus raptorius –
Cladotanytarsus conversus +
Ablabesmyia flavida +
Camptocladius stercorarius –
Paratendipes albimanus ●

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THE ACTIVITY PERIODS OF THE POPULATION OF PARAGYMNOMERUS SPIRICORNIS (SPINOLA). (HYMENOPTERA: EUMENIDAE)

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(Received June 15, 1973)

Abstract

On the basis of 1850 activity data observed at the entrance of 109 nests of *Paragymnomerus spiricornis* (SPINOLA) it can be stated that there is a main activity period falling between 4th June and 8th July which is preceded and followed by a pre- and a post-period, respectively.

The nest building habit (MÓCZÁR, 1939; 1960) and the developmental cycle (MÓCZÁR, 1962) of a wasp inhabiting the loess wall of the Tihany Peninsula in large populations have been discussed earlier in a number of papers. The correlation existing between the activity of the population and the microclimate has been treated by MÓCZÁR—ANDÓ—GALLÉ (1973). A possibility was offered between the 21st June and 16th August, 1971 to study the individual activity phases of the wasps living in large populations.

The activity of the wasps was moderated by the cooler and windy climate which prevailed between the 27th June and 3rd July, 1971. Unfortunately, the century's coldest July day fell on the 1st and 2nd. Notwithstanding the warmest days of the observation period with around 29 °C had a favourable influence than the similarly warm July of 1959 without the extreme temperature values (26,4 °C), thus, the final results of the investigations have not been heavily hampered with the above-mentioned strong fluctuation in temperature.

The maximum and minimum temperature values measured just in front of the loess wall are shown in the upper part of Fig. 1. On the days of observation we made recording for 19 hours (from 8 till 18 h). We closely observed the entrance of the funnel to 109 nests and recorded 1850 entrance and exit flights. The (quantity) number of activities observed in the funnels is shown in the perpendicular axis of Fig. 1, while the observation days are plotted on the horizontal axis. A graph demonstrates the activity data of the individual days. The broken line indicates that during the period of the observation (e.g. 22nd—27th of June) the recording was not continuous. It is revealed from the daily activity data observed in the funnels that the number of activities at the maximum temperature in the beginning of July coincided with the maximum activity of the wasps and it was twice as many on any day (5th—7th July) than previous to these days in 8 days (21st June—4th July) (527—482—522: 198).

On the first day of the observation (21st June), 2 ♂ flew in front of the loess wall, 12 ♀ were building craddles, 6 ♀ were bringing sawfly larvae. The activity of the wasps began weeks before. This is the first phase of the activity (I. or prephase), on the regular observation days the unfavourable weather prevailed (29th

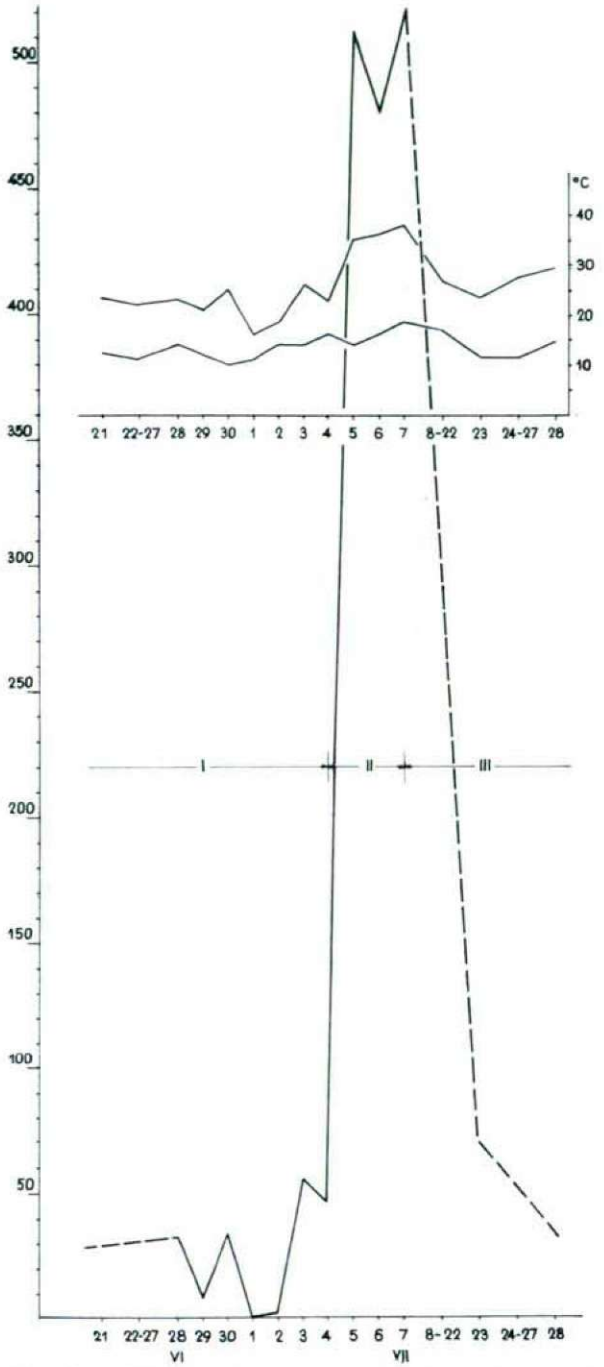

Fig. 1. Daily overall activity of *Paragymnomerus spiricornis* (SPINOLA) population, its stages (I, II III) and the temperature minimum and maximum values.

June—1st—2nd July) nevertheless acitivity shew a rising trend until the 4th of July (Fig. 1).

On the 5th of July the highest temperature maximum was accompanied by the corresponding maximum in wasp activity too, this is the second (II) phase, i.e. the main activity phase (5th—7th July).

Two weeks later (23rd July) the activity of the wasps fell back to the level perceived in the first phase. It must be the wasps' declining phase of activity, the third or post-phase. On the 16th of August not even one specimen of *Paragymnomerus spiricornis* (SPINOLA) was observed on the loess wall.

Thus, the activity of the population between the 4th of June, and 8th July may be divided into three phases, i.e. pre-, main and post-phase, because the highest number of specimens was active between these two dates. Furthermore, these two dates may also be regarded to be for any year the main period of flight because there was no apparent effect caused by the extreme values of temperature experienced during the time of observation.

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THE UNUSUAL BEHAVIOUR OF PARAGYMNOMERUS SPIRICORNIS (SPINOLA) (HYMENOPTERA: EUMENIDAE)

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Abstract

Experiments with marked Paragymnomerus spiricornis (Spinola) nests (Nos. 1—109) and wasps (53 specimens) proved that contrary to our earlier knowledge 14 waps entered into 2—3—4 strange nests, in four nests two wasps were observation at the same time. By revealing these most of our earlier ethological observations become unreliable and call for further experiments carried out with similar marking systems.

For many decades specimens of *Paragymnomerus (=Odynerus) spiricornis* (SPINOLA) have been nestling at the same site. Several contributions appeared on the ecological-ethological conditions of this population (MÓCZÁR, 1939—1962), on certain datails of behaviour (GIRAUD, 1863; MÓCZÁR, 1939; 1960a; 1961a; b; 1972; 1973). Reference was also made to the fact that two specimens of the same species have been found at the entrance of the nest where they (i. e. not the parasite and its host) fought (MÓCZÁR, 1960b). The following examination was carried in order to elucidate the details of intrusion into strange nests of this solitary wasp grouping into populations.

Method

Between the 21st of June, 1971 and the 16th of August, 1971 on the loess wall at the foot of Csúcshegy in the southern parts of the Tihany Peninsula for 17days seriatim all those funnels were marked with different colours in which active wasp was perceived. As a control beside the funnels we placed tiny flags numbered from 1 to 109 marked also with the same colour of paint (Fig. 1). Between the 28th of June and the 6th of July, 1971 we marked the females frequenting 53 funnels according to differently coloured dot and line combinations grouped into tens which marks also appeared on the funnels. The marking of the observed females is important as it had already been pointed out by LINSLEY et al. (1952) and MICHENER et al. (1955). The numbering of wasps was made on ice-cooled specimens (MÓCZÁR, 1960). The phases of activity of wasps visiting the marked funnels were recorded on tape-recorders between the 26th of June and 8th of July by Dr. L. GALLÉ, Mrs. Dr. B. HAJÁSZ, Miss M. KÁLMÁN and the author in groups of two for 19hours a day (8^h—18^h). Thus we obtained a huge amount of data from 109 funnels, which totalled 1849 phases of activity upon which fairly reliable inferences may be drawn.

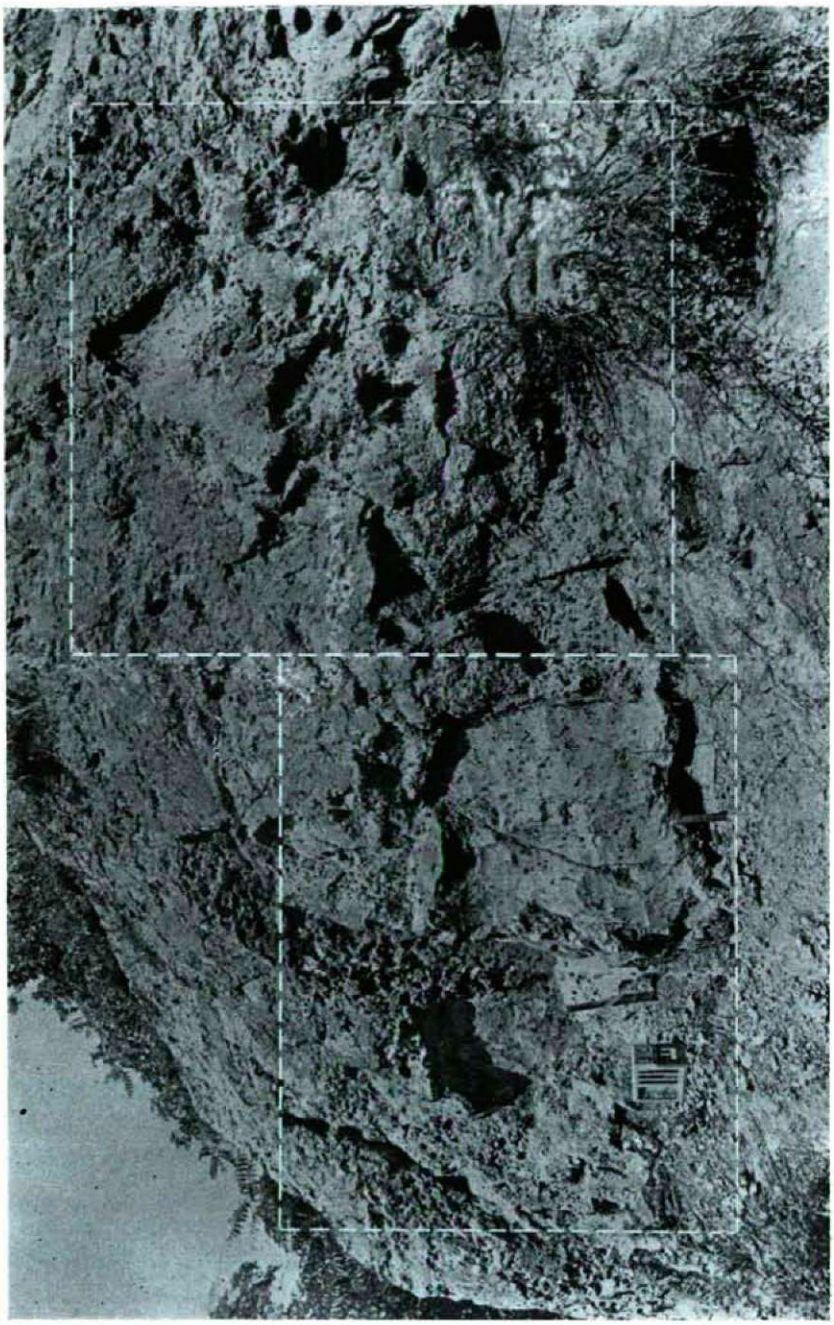

Fig. 1. The Tihany loess wall. Drawing 2 illustrate the turrets at the encircled parts.

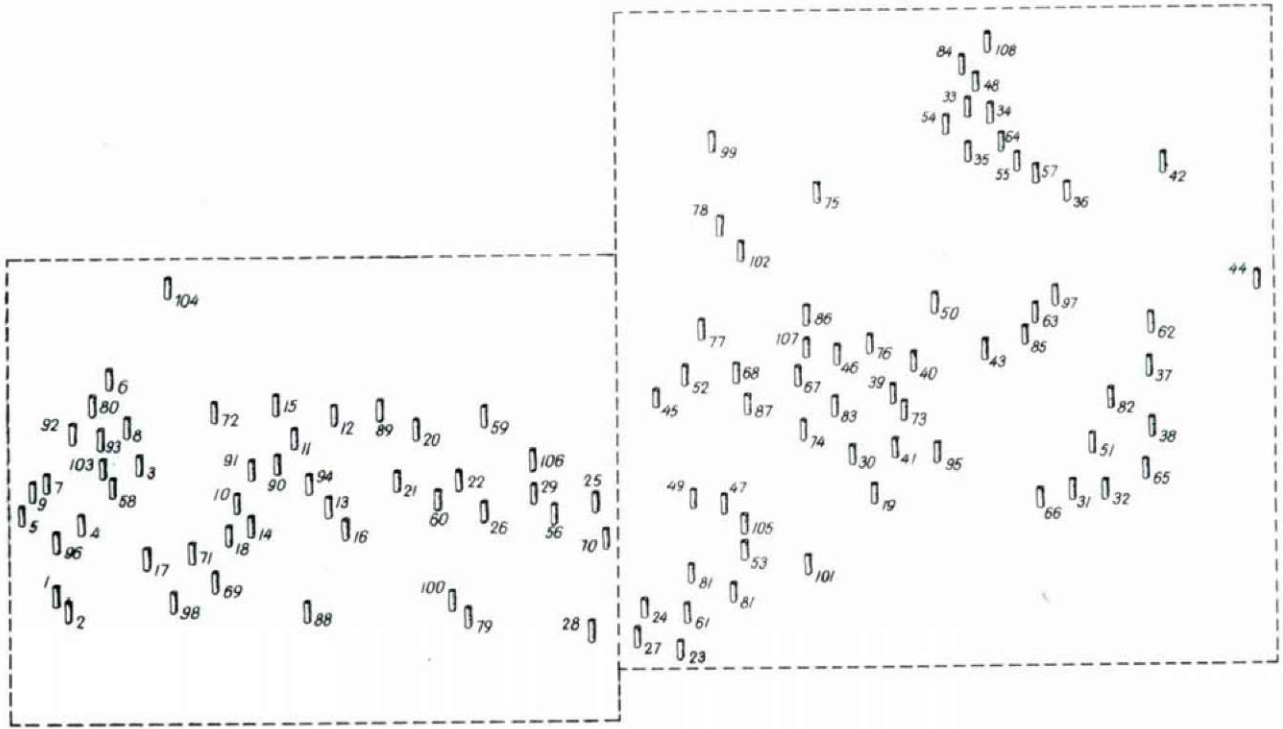

Fig. 2. The numbered turrets on two details of the loess wall.

Extract from the log-book of some nests:

Nests Nos. 3, 60, 84 and 95.

28th June: nest No. 3 was marked.

4th July, 14^{40}: the captured wasp, taken from the nest, was marked according No. 3 then was replaced on its funnel. A white on its back also indicated that the wasp found active on the 21st of June.

5th July, 11^{40}: Wasp No. 3 was building funnel No. 60, which was only one centimetre high, thus its second nest under our observation must have been started only today.

11^{50}—13^{33}: the same wasp observed in 14 occasions while it built nest No. 60, and brought out debris from inside.

13^{34}: one (it was not possible to identify whether it was a marked or unmarked specimen) wasp was active in nest No. 95.

13^{46}: wasp No. 3 was erecting the funnel No. 84.

13^{47}—16^{57}: wasp No. 3 was observed in 29 occasions while it erected the funnel No. 84 or entered, 6th July, 10^{44}—13^{03}: in 4 occasions we noticed wasp No. 3. to enter funnel No. 84.

14^{08}: activity was observed in nest No. 95. 7th July, 11^{45}: wasp No. 3 entered the ready funnel marked No. 95.

11^{46}—16^{12}: the wasp was captured to control marking and afterwards in 19 occasions we obserwed it to be active in funnel No. 95. While marking the funnel was damaged and cracked at the upper edge, but after some hesitation the wasp resumed the building of the funnel.

23rd July, 15^{00}—15^{52}: in 7 occasions we observed wasp No. 3 to enter nest No. 95.

28th July, 10^{03}—15^{10}: in 19 occasions we observed wasp No. 3 to repair funnel No. 95, finally the wasp partly demolished the funnel and blocked up the entrance.

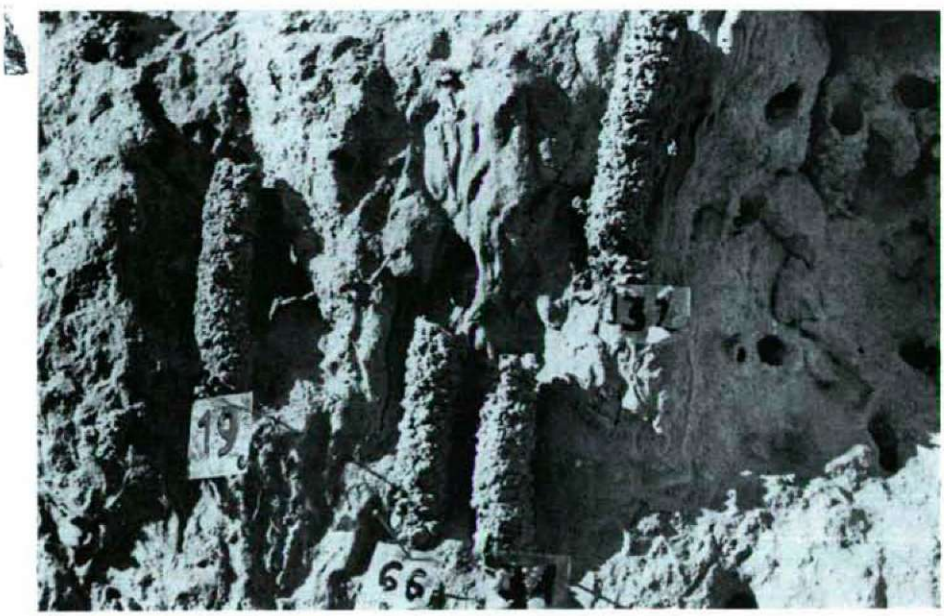

Fig. 3. Right upper detail of the loess wall with some turrets and flags.

Wasp. No. 3 was observed for 38 days on the loess wall and its activity was continuously recorded for 7 days. Surprisingly the wasp was active in four funnels: Nos. 3, 60, 84 and 95. For 6 days its work was intensely watched: on the 4th it spent a short time in nest No. 3, on the 5th two hours in nest No. 60, during a whole

afternoon and the following forenoon it spent its time in nest No. 84, while in three different days it was building the funnel to nest No. 95, or only flew in or out. In other words, the wasp has not completed a single craddle between the 4th and 7th of July, nor has it brought sawfly larvae in it, but it entered even strange nests where it actively worked for a prolonged time (7th—28th July). Out of these nests the wasp only built the one marked No. 60 for certain, its visits, on the other hand, included those nests which had already been marked, i.e. those with funnels being strange to it. On the 5th—6th the number of the wasp was left unobserved though actively worked in nest No. 95, it is most likely that it was wasp No. 3.

Nest No. 39.

28th June, 14^{10}: a wasp began to build a nest and to raise its funnel.
15^{00}: the base of the funnel was marked.
29th June, 16^{00}: the funnel is finished the upper wet part is dry.
3rd July, 13^{10}: the above funnel was numbered, the wasp captured from it has b orne two white flecks which indicate that it had already brought sawfly larvae on the 21st of June. This time mark No. 39 (yellow, the reverse of No. 1) was painted on its back.
15^{07}—17^{10}: it was observed several times to fly in and out.
17^{15}: it entered the funnel, but immediately it returned onto and edge turning round backed into the nest, probably for spending the night in.
4th July, 14^{06}: it flew in.
17^{30}: it went in then came out again to turn around and backed into the funnel.
18^{52}: again it went into the funnel.
5th July, 15^{45}—17^{49}: several times it flew into the funnel.
6th July, 13^{37}: the funnel was raised by 1 cm, the wasp entered the opening.
13^{39}—17^{30}: the wasp was reasing the funnel in 15 occasions. In the meanwhile at 13^{49} and 14^{10} a much smaller *Odontodynerus d. deflendus* (SAUND.) stole mud globules from the funnel to fortify its own funnel.
7th July, 10^{20}: the wasp brought a yellow sawfly larva into the nest.
10^{59}—11^{05}: it flew in, but 20 sec. later it returned with the yellow sawfly larva and settled on the vegetation of the loess wall and finally it dropped the larva.
11^{10-11}: twice it entered the funnel, then it circled above the funnel.
11^{12}: another, this time a green sawfiy larva was brought out of the funnel.
11^{13-58}: 12-times it flew in and out of its nest meanwhile it circled above it, and flew off on shorter or longer distances.
12^{05}: flew in, soon after it left the funnel, another wasp entered it (!), thus, two wasps were active in one nest.
12^{06-07}: re-entered its nest.
12^{08}: it flew in, the former also soon entered the nest (now two wasps were in the nest).
12^{09}: both wasps came out, then soon both re-entered separately the nest.
12^{12}: one of the wasps captured from the nest has borne the number 53, after release it circled above the funnel, it could not enter the funnel because a glass vial blocked up the entrance.
12^{50}: the other wasp was also captured, it was marked No. 39, i.e. the original inhabitor.
12^{55}: wasp No. 39 flew in but soon returned.
13^{17}: wesp No. 39 flew into its nest, then returned and crawled into it backwards.
13^{29-34}: wasp No. 39 resumed building its funnel.
15^{02-15}: wasp No. 39 flew in and out several times.
23rd July, 12^{12}: wasp No. 39 transported two sawfly larvae into its nest.
14^{55-56}: the wasp was active in the nest.

Wasp No. 39 was observed for 33 days on the loess wall, and for 8 days its activity was recorded. According to the above, the wasp marked in nest No. 39 on the 21st June and even on the 23rd July brought sawfly larvae into the nest marked No. 39. Between 3rd and 6th July, on the 7th July in the forenoon was active alone in the nest, but between 12^{05-12} wasp No. 53 also entered the nest. Another extra-ordinary phenomenon was that wasp No. 39 brought out three sawfly larvae (7th July) from its nest, probably because before (in 10^{20-59}) a strange wasp intruded

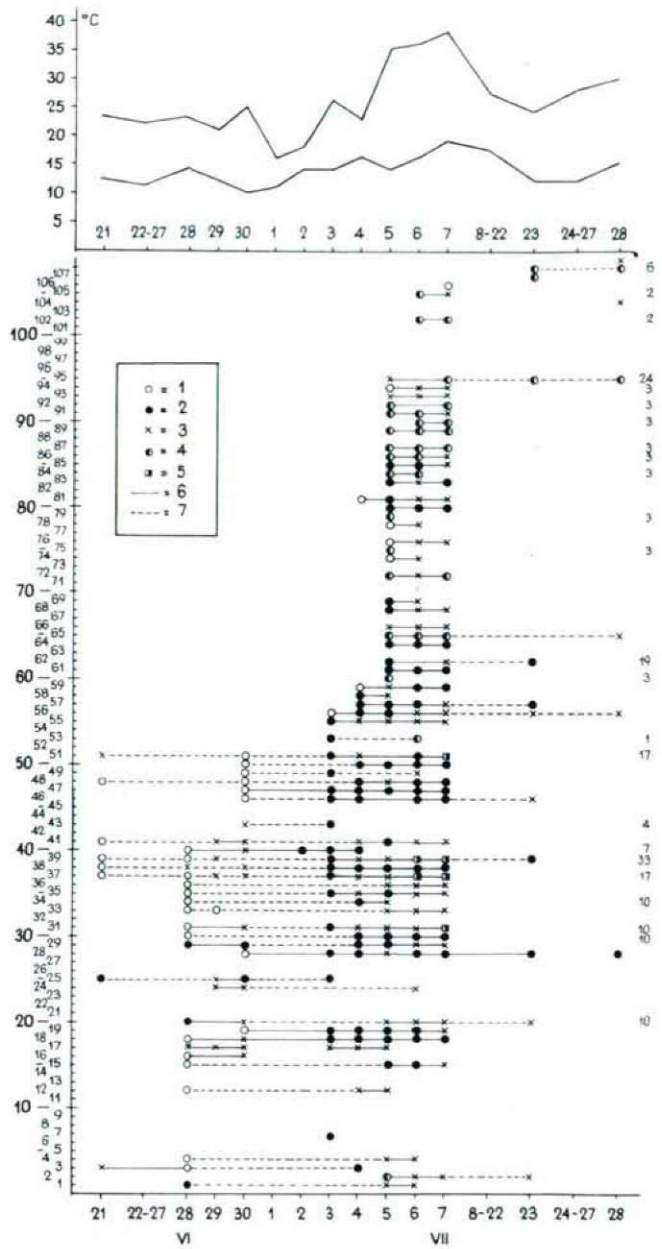

Fig. 4. Daily single activity observed in the numbered turrets. (Sign 1—5 see p. 170).

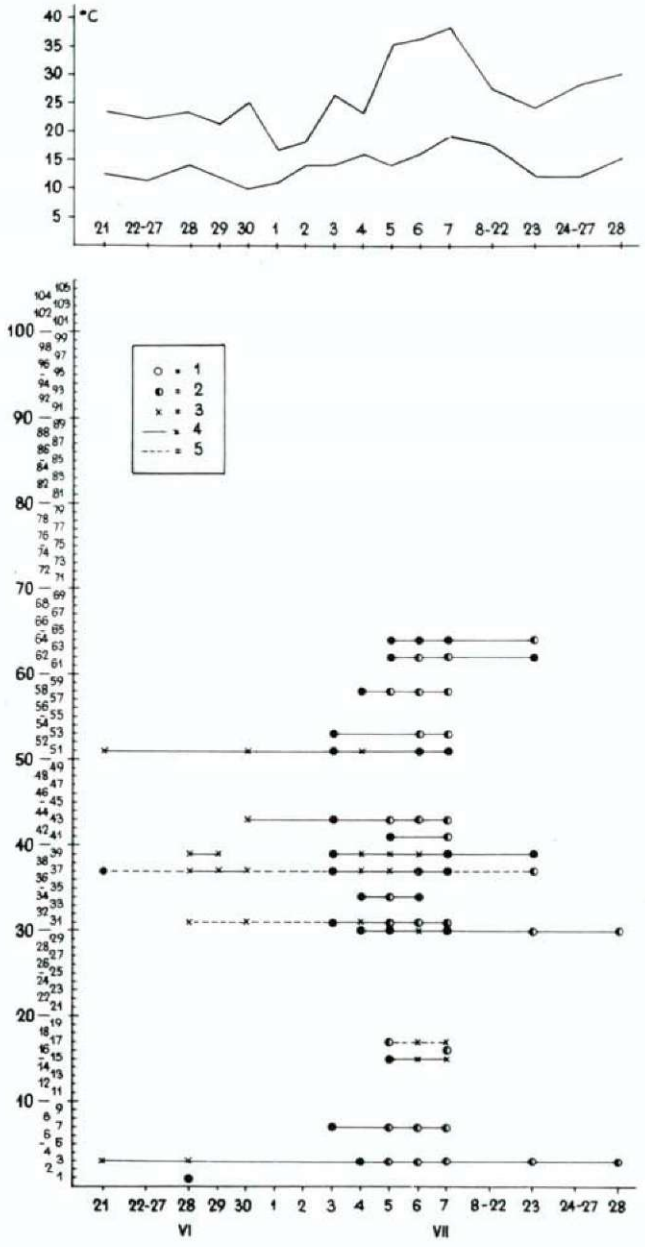

Fig. 5. Observed activity of the marked waps. (Sign 1—5 see p. 170).

the nest, which was unobserved by us. Subsequent to our observing the entrance of the strange wasp it did not throw out sawfly larvae from its nest because there was no open craddle within, and it is proved by the fact, that it soon started to dig another craddle after this incident (and raised the funnel). Only one point does not support this theory, i.e. at 13^{17} the wasp crawled inside the funnel backwards which generally mean ovipositing, of course, not every backward entrance means oviposition (cf. MÓCZÁR, 1973). There was no apparent reaction as to the stolen mud globules performed by *Odontodynerus* d. *deflendus* (SAUND.).

Summary to the observed nests Nos. 2, 17 and 72.

Wasp No. 17 was observed for 10 days on the loess wall, its activity was recorded in detail for 8 days. Owing to the fact that the wasp was first observed in the funnel, then in nest No. 2, it was obvious that it deserted nest No. 17 and favoured rather nest marked No. 2 (5th—23rd July), but the same wasp soon captured in nest No. 72 (5th July), and later though no identification was made most probably we observed the same wasp in nest No. 72 on the 6th and 7th July. Since because nest No. 2 was also visited, it is probable that wasp No. 17 tended two nests for three days (5th—7th July), or because we observed wasp No. 16 in nest No. 72 on the 7th July, this might have been that visitor the day before whose number remained unobserved. (Mark No. 17 cannot be mistaken for any other and the wasp was captured in two nests with only one minute difference in between).

Nests Nos. 7, 79 and 90.

Wasp. No. 7 was observed in 5 days, and recorded for 3 days. The wasp was in nest No. 79 (5th July) the next day it was working in the nest with a funnel No.90, here it most likely intruded as a stranger, on the second day it even brought a sawfly larva. In other words, the wasp was active at least in three nests at the same time.

Nests Nos. 30 and 108.

Wasp No. 30 was observed in 31 days and recorded for 6 days. After 16 days the wasp built a nest No. 108, and 5 days subsequent to this it was building another one. Its behaviour is normal.

Nest No. 31 (partly wasp No. 43).

The wasp of nest No. 31 was observed for 10 days and recorded in 7. For 9 days it worked alone, built its nest and brought sawfly larvae into it. In the afternoon of 7th July wasp No. 43 was also active in the nest together with No. 31, then the latter continued to work alone. The wasps did not fight with each other.

Nests No. 34 and 86.

Wasp No. 34 observed in 10 days and recorded for 4 days. It left its former nest on the 4th, on the 5th July in the afternoon it began to build another one (No. 86) into which brought a sawfly larvae, continued its activity there until noon next day. Early in the afternoon it returned to its former nest (No. 34) and worked there. Interestingly enough a wasp appeared in nest No. 86. On the 7th July for some two hours the wasp returned into its nest No. 34, in the afternoon in nest No. 86 again a wasp was present but we were unable to ascertain its number. On the 5th July at 13^{49} a wasp entered nest No. 34, it remains an open question whether it was wasp No. 34 or not? In any way its behaviour is not normal.

Nest Nos. 41 and 91.

The wasp of nest No. 41 was observed in 17 days and recorded in detail for 3 days. On the 5th July at noon the wasp was active in nest No. 41, in the afternoon it was captured in nest No. 91. Although on the 6th the number of the wasp was not controlled it is most likely that it stayed in nest No. 91, because on the 7th for certain we observed wasp No. 41 in nest No. 91, furthermore, a strange twice fought with it fiercely.

Nests Nos. 43, 75, 87 and partly No. 31.

Wasp No. 43 was observed in 8 days on the loess wall and recorded in detail for 5 days. The wasp was active in 4 nests, in two nests for 1 and 1/2 day, respectively, in nest No. 87 for 2 1/2 days. Nest No. 75 was only visited for very short periods of time, so under no condition could it build a craddle therein, in other words, it deserted its nest and started to build a new one, but before it had completed even one craddle, at least in two occasions intruded nest No. 31.

Nest No. 51.

Wasp No. 51 was observed in 17 days and recorded for 5 days. Its activity was normal until 16^{16} on the 7th of July, but between 16^{19} and 16^{26}, though no reference number is given in the log-book as to the wasp one must have been the owner of the nest, two wasps were in the nest, then it disappeared from our sight. No fight is recorded in the diary. The wasp apparently did not react to the stolen mud globules performed by an Odontodynerus.

Nests Nos. 53 and 105.

Wasp No. 53 was observed in 5 days and recorded in 3 days. The wasp was marked on the 3rd but then it disappeared. In the afternoon of the 6th July we observed it as it started to build nest No. 105. An hour later disappeared again. The following day at noon wasp No. 53 was captured in nest No. 39 where it spent 4 minutes, 5 minutes later it began to build a third nest. Thus, wasp No. 53 did not even build one craddle let alone bringing a sawfly larva into it, but it started to build a new nest, meanwhile it intruded a strange nest and spent 4 minutes with the owner (No. 39) of the nest.

Nests Nos. 58 and 89.

Wasp No. 58 was observed on the loess wall in 4 days, and its activity was recorded for 3 days. During this time it provided two craddles with sawfly larvae, then it began to dig a new craddle. It is somewhat strange what made the wasp leave nest No. 58 at 13^{16} on the 5th and work 24 minutes later (at 13^{40}) in a strange nest.

Nests Nos. 62. and 102.

Wasp No. 62 was observed in 19 days on the loess wall and recorded for 4 days. On the 5th it was active in nest No. 62, in the afternon on the 6th it visited the ready nest No. 102 and continued to build it. But on the 23rd July it again returned to its original nest. In spite of this, it is difficult to assume that on the 6th at 17^{22} and on the 7th at 17^{27} a wasp carrying sawfly larva was No. 62, it is more likely that it was a strange wasp which took possession of the deserted nest. Wasp No. 62 was active in nest No. 102 then 16 days later we observed it again in its original nest.

Nests Nos. 64 and 107.

Wasp No. 64 was observed in 29 days and recorded for 4 days. Between the 5th and 7th of July it built nest No. 64, on the 23rd nest No. 107 and brought a sawfly larva into it. Its activity is nomral.

The observed activity data are plotted on two graphs (Figs. 2 and 3). The horizontal axis on both show the days of observation, above the recorded minimum—maximum values of the weather. The vertical axis of Fig. 2 shows the numbered funnels, the same on the third figure displays the wasps marked with a combination of figures. The graph of Fig. 2 includes the partial data of a daily activity, in Fig. 3 the activity of marked wasps may be seen according to the following key: 1 — open circle — it was active in the funnel (flying in or out, erecting the funnel, bringing sawfly larvae), 2 — full circle — the wasp was active in its own nest (— the number of the wasp is identical with the number of the nest or funnel when it was captured), 3 — x — some real activity or the daily changing colour mark on the funnel, by which the series was conceived, 4 — half-full circle — the activity of a strange wasp (Fig. 1) or (Fig. 2) the wasp being active in a foreign nest, 5 — half-full square — activity of home or strange wasp observed only in one funnel, 6 —full line — continuous activity was observed for a number of days in one nest, 7 — broken line — on the respective days no observations were made, but wasp activity was probable.

The results of the observations

1. During this time 4 nests Nos. 31, 37*, 39 and 51 were invaded by strange nests in which the owner was at home, 12 wasps were captured in strange nests. From the latter, 7 wasps (Nos. 30, 34, 40*, 41, 58, 62 and 64) were active in 2 nests, 3 wasps (Nos. 7, 17 and 53) in 3 nests, 2 wasps (Nos. 3 and 43) in 4 nests.

2. In 3 wasps the second nest was built by the same wasp (nest No. 108 was built by wasp No. 30, nest No. 65 by wasp No. 40, nest No. 107 by wasp No. 64). Their activity is normal for no other wasp intruded their nests, and neither did they invade strange nests, the building of a second nest is normal, for during their lifetime one wasp generally builds several nests.

3. Only in two wasps could we prove that in the subsequent visiting of nests one was originally its own which it was building from the start (wasp No. 3 — nest No. 60, wasp No. 53 — nest No. 105). In further three wasps it is presumable that the nests are their own (wasp No. 34 — nest No. 86, wasp No. 40 — nest 108, wasp No. 64 — nest No. 107), all the other frequented nests were strange to the wasps.

4. Nests visited later in five occasions proved to be the meeting place of two wasps (nests Nos. 31, 37, 39, 41 and 51), i.e. they were inside at the same time (or a strange wasp intruded into the nest).

5. The meeting of strange wasps generally resulted in a prolonged fight, in only two occasions (nests Nos. 31 and 51) did we fail to observe any fight between the two wasps.

* Note: Wasps Nos. 37 and 40 have been discussed in detail elsewhere (MÓCZÁR, 1973).

6. Two wasps (Nos. 17 and 34) were active in two nests at the same time.

7. Two wasps (Nos. 34 and 62) were working in other nests, but returned some days later into their original contructions.

8. There is no correlation between the frequency of changing nests and the duration of the observation. For example:

No. of visited funnels	No. of observation days	No. of recorded days	No. of marked wasps
4	38	7	3
4	8	5	43
3	5	3	7
1	33	8	39
1	17	5	51
1	10	7	31

9. Some of the wasps are rather inconstant in nature, i.e. before they have finished even one craddle, they start to dig another one, in other words, they entered a strange nest (e.g. wasp No. 53).

10. Wasp (No. 53) working for a prolonged time in its nest may enter for a short time a strange nest, or a wasp spending a longer period of time in its nest may witness the visit of a strange wasp (wasp No. 43 invaded the nest of wasp No. 31). A possible explanation to this is a disorder in orientation.

11. Permanent change of nests is a more frequent phenomenon (wasp No. 17 into nest No. 72, wasp No. 41 into nest 91, wasp No. 62 into nest No. 102, wasp No. 7 into nests Nos. 79 and 90). The explanation is possibly in some environmental effect (such as unsuitable medium), the long duration between nest building and ovipositing, etc.

12. One wasp (No. 43) was active in four nests (Nos. 75, 87 and 31). One wasp (No. 17) was also active in three nests, at least intruded them (Nos. 2 then 72).

13. A wasp may intrude several nests (wasp No. 3 into nests Nos. 60, 84 and 95) and may stay there for shorter or longer periods of time.

14. The wasp shows no reaction to the fact that an *Odontodynerus* d. *deflendus* (SAUND.) has stolen building material from its funnel.

Summary

Between the 21 st of June and 16 th of July, 1971 we marked 109 *Paragymnomerus spiricornis* (SPINOLA) nests and 53 wasps with different combination of coloured marks, by this we were able to make 1849 recordings referring to behaviour. By our system of marking we could prove that 14 nests were invaded by strange wasps wherein they were building the nest or active in some manner. In four nests two wasps were together at the same time. At the meeting of strange wasps generally we observed a fight. The simultaneous activity of two wasps in one nest usually resulted in a return to their original nest after a few days. The above recordings clearly show that the activity of the wasps is by far not always is order and routin-like, as it has been suggested previously in literature, the conclusions

of which were founded on unmarked specimens of wasp. It is very likely that the situation will be different when conducting experiments with marked wasps. The system of activity of wasps quite frequently is upset. For some unknown reason the wasps perform activity which is sometimes the exact opposite what had been supposed in the sequence of nest building – oviposition – hoarding of food for the offspring – sealing the craddle. The above facts seem to support an earlier assumption (MÓCZÁR, 1960) which declared that wasps living in groups are more ready to accomodate themselves and quickly fined the next step in activity in a strange nest, e. g. they continue to build the funnel, collecting larvae as food for the offspring, completing the nest, etc. And this seems to be an important link between solitary and social life. The enumerated irregular activities cannot be answered as yet, the motives are yet hidden, to find correct explanation to these irregularities and to their motivation are the most important tasks of the future.

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ON ANOTHER NEW SPECIES OF THE GENUS METRIONOTUS MÓCZÁR (HYMENOPTERA: BETHYLIDAE: MESITINAE)

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Prepared in the Zool. Institute of the József Attila University Szeged

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Abstract

The author describes *Metrionotus egypticus* a new species (female) from Egypt and *M. hongkongensis* another one (male) from Hong Kong; with regard to the morphological characters and the proclinate type of (male) antennae transfers five species described by him in the genus *Heterocoelia* in the genus *Metrionotus*. The species are segregated by means of a key.

In the genus *Metrionotus* were originally included 18 species (MÓCZÁR 1970a, b). While treating the reach material of the Washington Museum send to the author kindly by K. KROMBEIN deemed it necessary to distinguish besides the "erect" and "proclinate" types of male antennae a "suberect" type, too. The males belonging here show on the antennae hairs which are always shorter than the breadth of the respective joint and are similarly as in the "erect" type, tolerably sticking, the hairs, however, strikingly longer than those on the antennae of "proclinate" type. Relying on these findings as well as on the basis of other morphological characters (head, sculpture of prothorax) it was indispensable to transfer five species classified (MÓCZÁR 1971) in the genus *Heterocoelia* in the genus *Metrionotus*. These species as well as the new ones from Egypt and Hong Kong are treated for the sake of a better understanding in a key.

Metrionotus MÓCZÁR

Metrionotus MÓCZÁR, 1970a, Acta Zool. Hung., *16*:201—202 ♀♂

The diagnosis may be completed by the followings: Mesonotum and scutellum usually finely shagreened. Antennal joints with erect or suberect hairs ("proclinate, in acute angle (Fig. 16)" to be deleted). Instead of flagellar joints "2—6" write: "3 or 2—6". To be replaced: Antennal joint 2 of "suberect" males always distinctly longer than half length of joint 3.

In accordance with this will be the key of Mesitinae genera (MÓCZÁR 1971:326) modified.

Key of females

1—7 remains unchanged (MÓCZÁR 1970b:436)

8 Head brownish black, lower face yellowish red along occipital margin, mesonotum dark reddish brown, pronotum yellowish brown, mesonotum, scutellum brownish black. Head distinctly longer than broad (25:22). Wings only sligtly

infuscated. Pronotum shagreened, hardly punctured. Eye separated from mandible by about half distance of its length (7:13). Smaller species 2.7 mm *yarrowi* MÓCZÁR

— Head, thorax, legs uniformly yellowish red. Wings brownish infuscated, base, band below stigma and apex white ..... 9.

9 Lateral spine of propodeum about one-third as long as length of propodeum medially (6:17). Antennal joint 2 two-thirds as broad as long (4:6), joint 3 half as broad as long (4:8). Eye separated from mandible by third-fourths distance of its lengthy (11:14). Head rectangular, as long as broad (36:36), narrow behind eyes. Half diameter of propodeal disc transversally shorter than length of propodeum medially (15:17). 4.5 mm *brevispinosus* (BENIOT)

— Lateral spine of propodeum longer, nearly as long as two-thirds of length of propodeum medially (7:11). Antennal joint 2 half as broad as long (2.4:5), joint 3 slender, its breadth shorter than its half length (2.5:6). Eye separated from mandible by about half of its length (7:6.5). Head distinctly longer than broad (34:30). Half diameter of propodeum transversally as broad as length of propodeum medially (11:11)3.7 mm *egypticus* sp. n.

Key of males

1 Antennae with extremely long, sparse and erect hairs, hairs distinctly longer than width of the joints; joints 2—6 usually narrower proximally than apically (distally); inner side of joints often concave, joint 2 about only half as long as joint 3 ..... 2.

— Antennae with long suberect hairs, hairs at most as long as width of joints or on last joints shorter; antennal joints 2—3 or 2—6 narrowed basally and apically and with convex sides, joint 2 always distinctly longer than half length of joint 3 ..... 6 respectively 8.

Point 2—7 remains unchanged with species *brevispinosus* (BENOIT), *africanus* MÓCZÁR, *szelenyii* MÓCZÁR, *wolfi* MÓCZÁR and *mocsaryi* MÓCZÁR (MÓCZÁR, 1970b:437).

8 Each of central area of propodeum (also distally) as broad as sublateral area or broader. Antennal joints 2—4 equal in length ..... 9.

— Each of central area of propodeum remarkably narrower than sublateral area. 10.

9 Lateral angles of propodeum reactangular, lying remarkably deeper than middle of hind margin, sides of propodeum parallel central, area as broad as sublateral one (4:4 viewed from above). Tergite 2 finely alutaceous basally and polished, 3—5 finely alutaceous and partly polished. Propodeum relative long, half breadth of disc shorter than length of propodeum (1:14).1.9 mm *minutissima* (MÓCZÁR)

— Lateral angles of propodeum with distinct short spine. But lyng only slightly deeper than middle of propodeum Central area distinctly broader than sublateral area (6: 5 viewed from above). Tergite 2 only basally shagreened, medially and distally polished and with very fine and scattered punctures, tergites 3—5 finely alutaceous. Propodeum relatively shorter, half breadth of disc shorter than length of propodeum (13:15). Mesonotum, scutellum remarkably shagreened. 2.5 mm *parvulus* (KIEFFER)

10 Tergite 2 only alutaceous, shagreened-granulated or partly polished and not punctured ..... 11.

— Tergite 2 finely or very finely punctured, sometimes alutaceous or finely shagreened baselly ..... 13.

11 Tergites 2—6 entirely shagreened. Head, thorax shagreened, head, pronotum with scattered and superficial, mesonotum without punctures. Head as long as broad. Anterior ocellus with a distinct, shining pit, outer sides of hind ocelli with narrow, shallow groaves. Clypeus with slightly curved anterior margin. 2.5—3 mm *alutaceus* (BENOIT)

— Tergites only basally shagreened, polished distally ..... 12.

12 Posterior angles of propodeum with distinct, but minute spines. Antennal joint 2 slightly shorter than 3 (4:5). Half breadth of propodeal disc narrower than length of propodeum medially (9:11). Head circular as broad as long (24:24), Longitudinal furrow of pronotum narrow. 2.8 mm *bouceki* (MÓCZÁR)

— Posterior angles of propodeum rectangular without separated spines. Antennal joints 2—3 equal in length. Propodeum rather long, half diameter of disc transversally nearly as broad as length of propodeum medially (8:9). Head slightly longer than broad (18:16). Longitudinal furrow of pronotum very narrow. 2.1 mm *carbonarius* MÓCZÁR

13 Pronotum and half disc of propodeum as long as broad, rectangular. Lateral spine of propodeum distinct nearly as long as half length of propodeum medially (3:4). Longitudinal furrow of pronotum very narrow. Tergite 2 alutaceous — shagreened basally, polished and very finely and very scatteredly punctured, tergite 3—5 alutaceous. 2.9 mm *hongkongensis* sp. n.

— Pronotum, half disc of propodeum not rectangular, remarkably broader than long ..... 14.

14 Tergite 2 only with very fine and very scattered punctures. Spine of propodeum short, rather, stout. Antennae brown. Pronotum distinctly shagreened with scattered and deeper punctures than in *biroi* (MÓCZÁR), margin of longitudinal furrow more in distinct. Propodeum distinctly longer than half breadth of disc (11:8). 2.6 mm *zuluensis* (MÓCZÁR)

— Tergite 2 finely and scatteredly punctured ..... 15.

15 Posterior angles of propodeum with remarkably slender spines, lateral sides slightly convex, spine about twice as long as broad basally and about one-third as long as length of propodeum (3:10). Brownish antennal joints 2 and 3 of equal length, joint 2 slightly broader than 3. 2.5 mm *biroi* (MÓCZÁR)

— Posterior angles or propodeum stumpy without distinct spine, lateral sides parallel. Antennae brownish, joint 2 only hardly shorter than 3, is joint 2 not broader than 3.2.8 mm *nigropicea* (MÓCZÁR)

Metrionotus egypticus sp. n.

♀. — Length 3.7 mm. Head, thorax, legs, antennae yellowish-red, antennal joints 4—13 black only ventral side of joints brownish red, abdomen black and especially segment 1 dark redish translucent, last tergite with small yellowish streaks laterally. Wings normal, brownish infuscated, with lighter basis, narrow apex and a lerge streak outside of cells. Body sparsely covered with short white hairs.

Head oval, slightly longer than broad (34 across clypeus and vertex: 30 across eyes), distinctly rounded towards occipital carina, surface shangreened and only superficially punctured, weakly shining, frontal sulcus only basally distinct, POL:

OOL = 5:4, hind ocelli separated from eyes by a distinctly longer distance than from each other (7:5), ocelli with a minute groove outside; eye oval and convex, longer than broad (13:10), separated from mandible by about half of its length (7:13); anterior margin of clypeus protruding in an arch with a narrow translucent margin, surface raised into a high and sharp, longitudinal keel medially; antennal joints 1—3 slender, remarkably longer than broad, flagellum only thickened in joints 6—8, flagellar joint 2 is the longest, flagellar joints 1 and 3, 4 gradually shorter, flagellar joint 2 more than twice longer than broad, antennal joints 4—11 only slightly longer than broad, length (and breadth) proportions of antennal joints 1—13 = 13 (4):5 (2.4):6 (2.5):4 (2.5):3.5 (2.5):3.5 (3):3.5 (3):3.5 (3):3.5 (3):3 (2.5):3 (2.5):3 (2):4 (2).

Pronotum only three-quarters as long as broad (12 medially:19 in front), anterior angles rounden, lateral sides parallel and diverging before tegulae, posterior margin emarginated, surface shagreened and only superficially punctured, hardly shining, longitudinal furrow narrow. Mesonotum, scutellum shagreened, only weakly shining, parapsidal furrows only slightly distinct notauli deep, arched, longitudinal furrow of mesonotum not present. Mesonotum separated from scutellum by a transversal groove and by a pair of pits laterally. Half diameter of propodeal disc as broad as its length medially (11:11), lateral sides hardly diverging, posterior margin with acute spine laterally, this nearly as long as two-thirds of length of propodeum medially (7:11), all carinae and areas distinct, sublateral areas finely and sparsely wrinkled transversally, with proportions of central: sublateral: lateral areas = 4:5:2 (distally). Tergite 1 polished with some fine punctures, tergite 2 polished, shagreened baselly with distinct but scattered punctures, 3—6 shining and partly finely alutaceous.

♂. — Unknown.

Specimen examined: "Wadi Feran 4.3.35 Sinai W. Wittmer", "Col. Alfieri Egypte", Anastase Alfieri collection 1965", "No 442" 1 ♀ holotype, Mus. Washington Cat. No. 73279.

Similar to *Sulcomesitius africanus* MÓCZÁR (1970b) but differs chiefly by following characters: mesonotum without longitudinal furrow, abdominal tergite 2 remarkably scatteredly and more finely punctured.

Metrionotus hongkongensis sp. n.

♀. — Unknown.

♂. — Length 2.9 mm. Black, mandibles, tengulae brown, tarsi light brown, antennae and legs partly dark brownish. Wings normal, only weakly infuscated across radial cell to the hind margin of fore wing. Veins light brown. Body, especially head behind eyes and abdomen covered with white hairs. Antennae with long subrect hairs, hairs at most as long as width of joint only on last joints distinctly shorter.

Head only slightly longer than broad in front (24 together with clypeus : 21 across the eyes), strongly thickened behind eyes lateral sides distinctly convergent, posterior angles obtuse, occipital carina distinct; surface shagreened with larger but superficial punctures, frontal sulcus indistinct. POL: OOL = 4:3.5, hind ocelli separated by equal length from each other hand from eyes, outer sides of hind ocelli only with narrow grooves; eye very convex, short, about as long as broad (8:7), eye separated from mandible by about one-third of its length (3:8); anterior

margin of clypeus rounded, surface raised longitudinally in a sharp keel medially; antennae very long, reaching to abdominal segments, antennal joint 1 as long as joint 3 but remarkably thicker, joint 2 remarkably long nearly as long as joint 3 distinctly thickened medially and narrowed basally and apically, with convex sides, joint 2, 4—7 equalin length, length (and breadth) proportions of antennal joints 1—13=6 (2.5):5 (2):6 (2.5):5 (2.5):5 (2.5):5:5:4:4:4;4 (2):5.5 (1.5):6 (1.5). Pronotum rectangular as long as broad (12:12), lateral sides slightly concave on its three-quarters length before diverging to tegulae laterally, posterior margin nearly straight only slightly emarginated, longitudinal furrow very narrow, surface shagreened and superficially punctured. Mesonotum and scutellum shining, finely shagreened. Parapsidal furrows absent notauli of mesonotum deep, remarkably converging distally, medial longitudinal furrow not developed. Mesonotum separated from scutellum by a deep groove and by a deep pit on both sides. Propodeum as long as half bradth of disc (8:8), lateral sides slightly, posterior angles with distinctly projected acute spines, spine nearly as long as half length of propodeum medially (3:8), all carinae and areas distinct, sublateral area weakly shining, finely transversally striated. Abdomen smooth, shining, tergite 1 polished, base of tergite 2 and tergite 3 alutaceous-shagreened, tergite 2 only with few very fine and very scattered punctures, tergites 4—5 aluceous.

Specimen examined: "Hong Kong: N. T. Yuen Long District Castle Pk. For. Sta area, 5. VIII. 1964", "V. J. Voss Collector Bishop" 1 ♂ holotype, Bernice P. Bishop Mus. Honolulu Cat. No. 10,267.

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THE FLOWER-VISITING ACTIVITY OF APOIDEA ON LUCERNE (HYMENOPTERA: APOIDAE)

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The work was completed at the Zoological Department of the Attila József University, Szeged

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Abstract

The flower visiting of *Bombus agrorum* F., *Megachile argentata* F. and *Melitturga clavicornis* LATR. per minute was more frequent than of other species, but *Megachile argentata* F., *Megachile centuncularis* L. and *Eucera pollinosa* SMITH. opened up the highest number of flower heads. On the basis of abundancy (TANÁCS, 1974) and activity of the observed species *Andrena ovulata* K. *Melitta leporina* PZ. and *Melitturga clavicornis* LATR. proved to be the most useful species on the lucerne fields in the environs of Szeged. Although the flower visiting of honey-bee is significant, its flower opening is almost neglectable, which can be explained by its nectar collecting activity.

Introduction

It is common knowledge that the flowers of lucerne may open up automatically (LESINS, 1950), but these produce seeds in smaller number further hampered by a decrease in viability than those pollinated by alien means (BŐJTŐS, 1951). Apoidea as a feeding-biological life-form represent the sustinent elements of the biocenose (SZELÉNYI, 1960). With my observation I aimed at an assessment of the activity of this group of insects. Locality of experiments were the lucerne fields in the environs of Szeged, in southern Hungary.

Methods

My flower visiting observations were carried out during the swarming maximum (at about 13 h) of Apoidea with a view to MÓCZÁR's (1959b) method. The most frequently occurring 10—12 species of wild bee were observed for a period of one minute each. I noted down the number of the visited flowers and how many of these were opened. These observations have been extended to the activity of honey-bees, too.

My observations were carried out on the lucerne fields in the vicinity of the airport (Szeged) on the following days: 23rd—27th July (every day), 2nd and 5th August in 1971, 22nd—23rd, 25th 27th, 30th July, 1st—2nd, 11th August in 1972.

The lucerne fields of Újszentiván is situated some 18 km SE of Szeged not far from the Hungarian—Yugoslavian—Roumanian border, the dates are as follows: 21st—22nd, 28th—31st July, 3rd—4th August in 1971; 22nd—23rd, 25th, 27th—30th June, 1st—2nd, 4th July in 1972.

I have also noted down the weather conditions of days on which observations were made.

Results

Upon the following factors I have evaluated the flower-visiting activity of 33 wild bee species in the years of 1971 and 1972: number of flowers visited per minute, percentage of opened flowers, and the number of actually opened flowers per one minute (Table 1).

Table 1. The flower-visiting activity of wild bees on the lucerne fields in the environs of Szeged in 1971—72

Species	I	II	III	I	II	III	I	II	III
	1971			1972			average		
Bombus agrorum F.	20	55,55	11,00	17	57,63	9,71	18	57,01	10,05
Megachile argentata F.	—	—	—	17	91,66	15,13	17	91,66	15,13
Melitturga clavicornis LATR.	18	63,98	11,25	15	75,81	11,06	16	70,38	11,16
Bombus lapidarius L.	18	61,42	10,75	14	73,24	10,45	16	67,68	10,58
Eucera clypeata ER.	18	50,94	9,00	15	82,69	12,28	16	71,97	11,30
Megachile centuncularis L.	—	—	—	16	85,48	13,25	16	85,48	13,25
Andrena variabilis SM.	16	48,93	7,66	—	—	—	16	48,93	7,66
Bombus terrestris L.	15	70,00	10,50	15	69,85	10,55	15	69,98	10,53
Bombus silvarum distinctus VOGT.	14	63,64	8,75	15	59,21	9,00	15	61,06	8,88
Bombus hortorum L.	—	—	—	15	44,44	6,66	15	44,44	6,66
Melitta leporina PZ.	15	77,11	11,53	13	79,34	10,57	14	78,44	11,00
Halictus calceatus SCOP.	—	—	—	14	48,15	6,50	14	48,15	6,50
Eucera pollinosa SMITH	—	—	—	13	80,38	10,50	13	80,38	10,50
Andrena labialis K.	15	64,65	9,38	8	75,28	6,09	11	69,27	7,47
Halictus malachurus K.	9	57,14	4,00	10	55,74	5,67	10	56,54	5,40
Halictus leucosonius SCHCK.	10	57,14	5,33	—	—	—	10	57,14	5,33
Andrena flavipes PZ.	12	66,00	7,61	7	85,06	6,17	9	72,99	6,92
Halictus eurygnathus BLÜTHG.	8	85,71	7,20	7	75,00	5,57	8	79,79	6,25
Andrena ovatula K.	8	81,81	6,75	7	73,03	5,33	8	76,14	5,80
Halictus patellatus MOR.	—	—	—	6	70,83	4,25	6	70,83	4,25

I = number of flowers visited per minute
II = percentage value of flower opening
III = value of actual flower opening per minute

It may be established that the flower visiting of *Bombus* species per minute is very high, but *Megachile argentata* F., *Megachile centucularis* L. and *Eucera pollinosa* SMITH. appear to be the most useful species because they open up the highest number of flowers per minute. It is explained by the fact that the high number of visited flowers shew a greater percentage of opened flower heads. A comparison of these results with the country-wide values (MÓCZÁR, 1959b) is shown in Tabl 2.

The flower-visiting values per minute in the case of the same species are very close to each other. Difference of some significance is only observed in *Megachile argentata* F. The actual flower-opening values vary more or less in several species. It was found that the values of both flower-visiting and opening with identical species in the environs of Szeged were generally higher than those in 1954—55—56. It may well be explained by the obvious reason that Szeged and its environs are the sunniest regions of Hungary, consequently, they are warmer in climate, these make it possible for Apoidea to increase their activity.

Table 2. The comparison of flower-visiting and actual flower-opening values per minute of 1954—56 and 1971—72

Species	flower visiting per min		actual flower opening per min	
	I	II	I	II
Melitturga clavicornis LATR.	17	16	15,4	11,2
Megachile centuncularis L.	15	16	14,6	13,3
Eucera clypeata ER.	14	16	11,1	11,3
Eucera pollinosa SMITH	11	13	9,4	11,5
Megachile argentata F.	11	17	10,8	15,1
Andrena ovatula K.	6	8	4,9	5,8
Andrena flavipes PZ.	7	9	4,3	6,9
Melitta leporina PZ.	11	14	9,4	11,0
Bombus lapidarius L.	12	16	10,8	10,6
Halictus eurygnathus BLÜTHG.	7	8	5,2	6,3
Bombus terrestris L.	13	15	7,2	10,5
Bombus agrorum F.	—	18	—	10,1

I = MÓCZÁR (1959b) Country-wide data for 1954—55—56 (excluding those of country Csongrad)

II = own data for the environs of Szeged for 1971—72.

The flower opening of lucerne by *Apis mellifera* L. is successful only when the bees collect pollen, for during the time of nectar collecting they hardly ever open the flower heads (MÓCZÁR 1961a). According to BENEDEK, MANNINGER and DÉVAI (1971) bees visit lucerne flowers for the sheer purpose of nectar inbibition. The younger bees in their early days open the flowers up to 75—100 per cent (BÖJTÖS, 1962). In some special areas poor in flora, or in semi-arid spots the honey-bees appear to be the main pollinators among Apoidea (BOHART, 1957; PETKOV, 1967; VANSELL and TODD, 1946). I observed for a period of 50 minutes the activity of honey-bees during which I recorded 895 flower visitings, which means 17.9 visits per minute. The number of actual flower opening per minute is 0.5. During my observations the honey-bees collected almost exclusively nectar, and not pollen, thus, these records substantially support the observations mentioned by MÓCZÁR.

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OBSERVED CASES OF OS MALARE BIPARTITUM IN HUNGARIAN PALEOANTHROPOLOGICAL FINDS

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Abstract

Os malare bipartitum was found to occur in 10 cases among 1860 palaeoanthropological finds dating from the Middle European Copper Age to the Hungarian Middle Age, and primarily from the first millenium A. D. Three of these cases were of a Mongoloid nature. It appears obvious that a congenital anomaly is involved; there are no sexual differences in its occurrence, but it was observed more frequently on both sides of the splanchnocranium simultaneously. The frequency of 0.54% seems low compared to the literature data, but at the same time supports observations as to the extreme rareness of this anomaly.

In the study of palaeoanthropological material, besides the establishment of the metrical characteristics the observation of the non-metrical (morphological) variations (anatomical variations, pathological symptoms) too is becoming increasingly more important, since these permit the ascertainment of differences between individual populations (BROTHWELL, 1959). The observation of ten characteristics is proposed in the literature (BROTHWELL, 1963). Os malare bipartitum rtoo can be regarded as such a characteristic.

This congenital anomaly can be observed on the cheek bone (os malare), and arises through its bipartition by a suture. According to Virchow, two types can be distinguished:

1. division into an upper and a lower part by a transverse suture, and
2. division into an anterior and a posterior part by a vertical suture (FEHÉR, 1937).

Its formation has been explained by the occurrence of several ossification centres, though the presence of these has not yet been confirmed (MARTIN and SALLER, 1959). The phenomenon was first described by SANDIFORT in 1779 (FEHÉR, 1937), and has been mentioned since by a number of authors. It was termed by HILGENDORF and DÖNITZ os japonicum, by VIRCHOW os malare bipartitum (RANKE, 1881), by GRUBER os zygomaticum bipartitum (GRUBER, 1873a), and by BÄLZ os ainoicum (MARTIN and SALLER, 1959). The nomenclature os malare bipartitum was first used by MATIEGKA (1899).

In addition to the bipartite cheek bone, os malare tripartitum too can occur very rarely. This was first described by SPIX (1815), and later reported by other authors as well. Thus, GRUBER, RICCARDI, RUGGERI and CALORI describe its occurrence in human, and FLESCH and HRDLIČKA in orang-utan skulls (GRUBER, 1873b; CALORI, 1893).

It emerges from the literature references that the phenomenon of the bipartite cheek bone has been known for more than 150 years, and it is not surprising, there-

fore, that many populations have since been subjected to study with regard to the observation of its occurrence. Virchow found one such anomaly in 800 Bavarian skulls (RANKE, 1881), and HILGENDORF two cases from among 11 Japanese skulls, while DÖNITZ described it in Aino skulls (MATIEGKA, 1899). ELLIOT—SMITH and WOOD—JONES (1910) found seven cases in a large Egyptian series. MATIEGKA (1899) recognized it in one male skull, and gives the detailed literature of this anomaly.

In European populations it occurs with a frequency of 0.15—10.25% (FEHÉR, 1937).

The investigations of NAKANO, KOGANEI, HASEBE, ADACHI and TOLDT indicate that its frequency of occurrence in Japanese skulls is 3.5% (FEHÉR, 1937).

It has been examined in Aino skulls by BARTELS, BÄLZ, DÖNITZ, VIRCHOW, KOPERNITZKY, KOGANEI, LE DOUBLE, TARENECZKY, HABERER and TÖRÖK (FEHÉR, 1937; MATIEGKA, 1899).

Os malare bipartitum has also been found in a smaller material among Chinese, Koreans and extinct Peruvians, while only two cases have so far been described among Negroids (MARTIN and SALLER, 1959).

HRDLIČKA and RUSSEL found a frequency of only 0.06% in North-American Indians.

At any event, the presumed greater frequency in the Mongoloid races induced research workers to describe bipartite cheek bone as os japonicum (HILGENDORF and DÖNITZ) and os ainoicum (BÄLZ). In this way it was wished to indicate that this anomaly should be treated as a characteristic of humans belonging to the Mongoloid races. At the same time, MARTIN and SALLER (1959) point out that this suture anomaly occurs too rarely among the Mongolids main-races for it to be treated as specific for them. This also appears to be supported by the fact that the frequency found in Japanese skulls has a range 0—5.08%, whereas in certain cases among Europeans it can even attain 10%.

Hungarian material has been examined by LUSCHAN, MÉHELY and FEHÉR; the former two authors found it to be more frequent, and the latter a frequency of 0.15% (FEHÉR, 1937).

Materials and Methods

The Department of Anthropology in A. J. University, Szeged possesses several thousand authenticated palaeoanthropological finds; in addition to the customary anthropological evaluation, therefore, it was also possible to pay attention to this anomaly.

The finds were examined by the technique of MARTIN and SALLER to establish the following measurements: greatest length of the skull, the greatest width of the skull, the basion-bregma height, the width of the malar arch, the height of the upper face, the length and width of the palate, and the height and width of the orbit. The dimensions of the os malare and the sutural bone separated by the transverse suture were also established in the following way:

Greatest height of the os malare: the straight-line distance of the highest point of the zygomaticofrontal suture from the lowest point of the zygomaticomaxillary suture.

Upper width of the os malare: the straight-line distance between the highest points of the zygomaticomaxillary and zygomaticotemporal sutures.

Lower width of the os malare: the straight-line distance between the lowest points of the zygomaticomaxillary and zygomaticotemporal sutures.

Greatest length of sutural bone: where found.

Greatest height of sutural bone: where found.

The taxonomic determination is reported on the basis of the method of LIPTÁK (1972).

Finally, the dimensions, the most important indices and the results of the taxonomic determination are tabulated.

The more detailed description of the observed cases is as follows:

Most important measurements of skulls with os malare bipartitum

Measurements and indices	Skull inventory numbers, according to sex									
	Males					Females				Child
	1920.	981.	52.382.1.	257.	4076.	1717.	1804.	864.	861.	1175.
Glabello-occipital length	191	180	188	177	173	—	167	176	180	161
Maximum breadth of skull	152	161	139	146	148	143	134	143	130	—
Basion-bregma height	126	129	131	137	138	117	122	127	—	—
Cranial index	79,6	89,4	73,9	82,5	85,6	—	80,2	81,3	72,2	—
Breadth-height index	82,9	80,1	94,2	93,8	93,2	81,8	91,0	88,8	—	—
Bizygomatic breadth	145	142	126	133	130	121	126	120	—	—
Upper facial height	80	70	63	76	67	70	70	64	69	50
Upper facial index	55,2	49,3	50,0	57,1	51,5	57,9	55,6	49,2	—	—
Orbital breadth	40	37	39	37	36	43	39	41	39	34
Orbital height	37	32	30	30	32	39	36	33	30	30
Orbital index	92,5	86,5	76,9	81,1	88,9	90,7	92,3	80,5	76,9	88,2
Palatal length	49	45	46	55	46	50	40	49	46	—
Palatal breadth	40	44	41	40	39	41	40	40	36	—
Palatal index	81,6	97,8	89,1	72,7	84,8	82,0	100,0	81,6	78,3	—
Height of os malare (right)	61	—	45	—	48	47	52	50	—	—
Height of os malare (left)	54	—	45	—	47	47	50	47	—	35
Upper breadth of os malare (right)	50	—	—	—	—	43	—	46	—	—
Upper breadth of os malare (left)	50	—	38	—	42	—	37	44	—	34
Lower breadth of os malare (right)	27	—	—	—	—	38	—	26	—	—
Lower breadth of os malare (left)	32	—	18	—	30	32	17	27	—	18
Height of sutural bone (right)	12	—	—	—	—	9	10	9	—	—
Height of sutural bone (left)	—	—	9	—	7	—	7	—	—	7
Length of sutural bone (right)	32	—	—	—	—	36	—	29	—	—
Length of sutural bone (left)	30	—	18	—	31	—	15	—	—	21
Result of taxonomic determination	b	p—sa	crA—am	t	crB	—	p—x	crB—x	n	—

Explanation of symbols: b = Bajkal, p = Pamirian, sa = Sajanic, crA = Cromagnoid-A, am = Atlantomediterranean, t = Turanid, crB = Cromagnoid-B, n = Nordic, x = unknown.

1. Skull no. 1920. Site of find: unknown. Archaeological age unknown, but because of the mongolid features (Fig. 1, 1—2) probably Avar Period. A male of mature age. Bilateral os malare bipartitum, where the transverse suture is obliterated in both cases (Fig. 1, 3). Palatine, maxillary and mandibular tori (Fig. 1, 4—5) are to be found on the skull, with two os epiptericum on the left side. From a taxonomic viewpoint it can be identified with the Bajkal race.

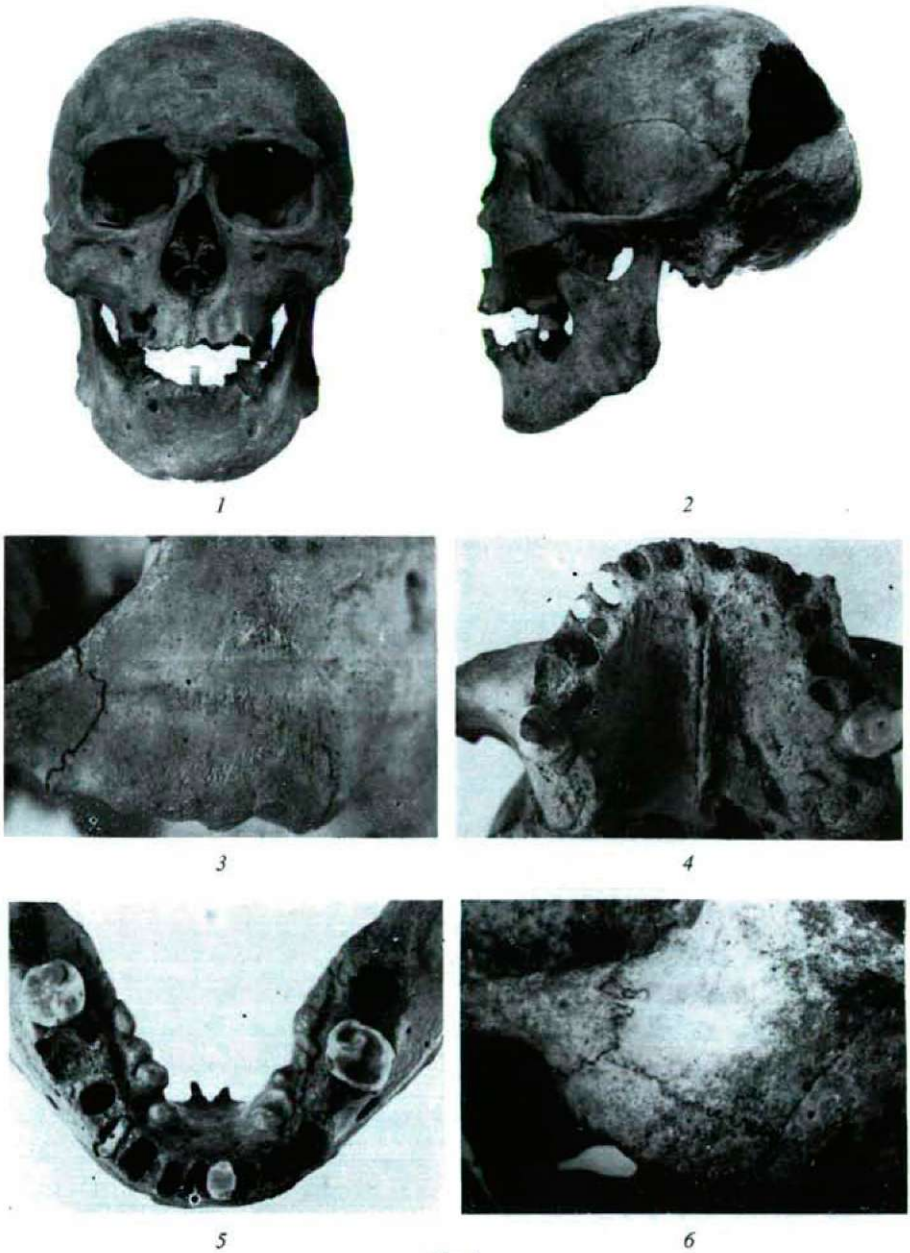
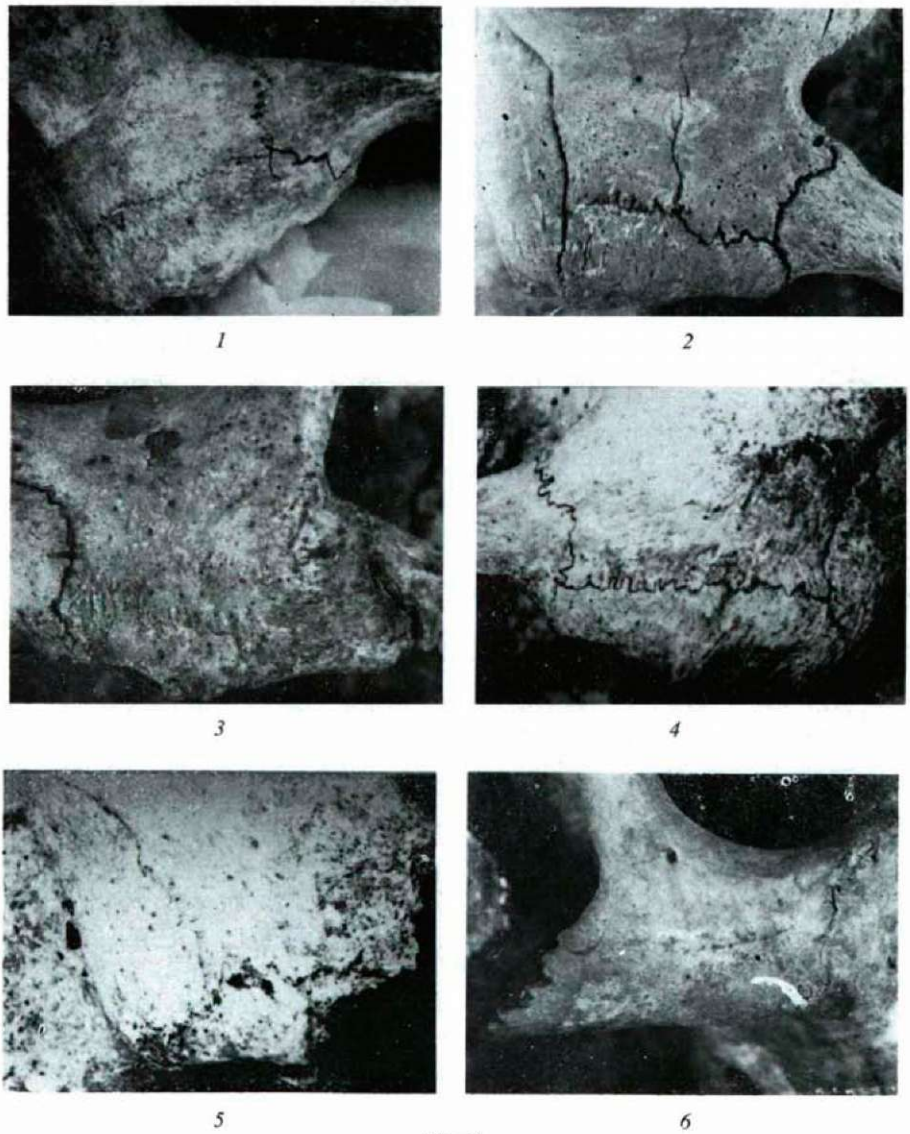


Fig. 1

2. Skull no. 981. Site of find: Adorján-Vata farm (Yugoslavia), grave no. 30, Avar Period. The find is in the collection of the Vojvodanski Muzej, Novi Sad, and was reported earlier (BARTUCZ and FARKAS, 1957). A male of mature age. Bilateral os malare bipartitum can be found on the skull (Fig. 1, 6 and 2, 1). From a taxonomic viewpoint it is a mixed variant of the Pamirian and Tungid (low-faced Mongoloid) races, i.e. Europeomongoloid.

3. Skull no. 52.382.1. Site of find: Orosháza-Rákóczi site, grave no. 232, Arpadian age. A male of adult age. Os malare bipartitum on the left side (Fig. 2, 2), with Worm-type bones in the lamboid suture. A mixed variant of the Cromagnoid-A and Atlantomediterranean races (LIPTÁK and FARKAS, 1962).



1 *2*

3 *4*

5 *6*

Fig. 2

4. Skull no. 257. Site of find: Zombor—Bükkszállás (Yugoslavia), grave no. 61, 15th—17th century. The find is in the collection of the Vojvodanski Muzej, Novi Sad. A male of mature age. Os malare bipartitum can be found on both sides, but that on the left side is extensively damaged (Fig. 2, 4—5). A metopic suture can be observed on the os frontale. According to BARTUCZ (1960), the find exhibits Turanoid features, i.e. it is Europeomongoloid.

5. Skull no. 4076. Site of find: Vedresháza, grave no. 64, Avar Period. A male of mature age. Ossified os malare bipartitum on the left side (Fig. 2, 3). Os epiptericum and a Worm-type bone can be found on the skull. It exhibits features of the Cromagnoid-B taxon.

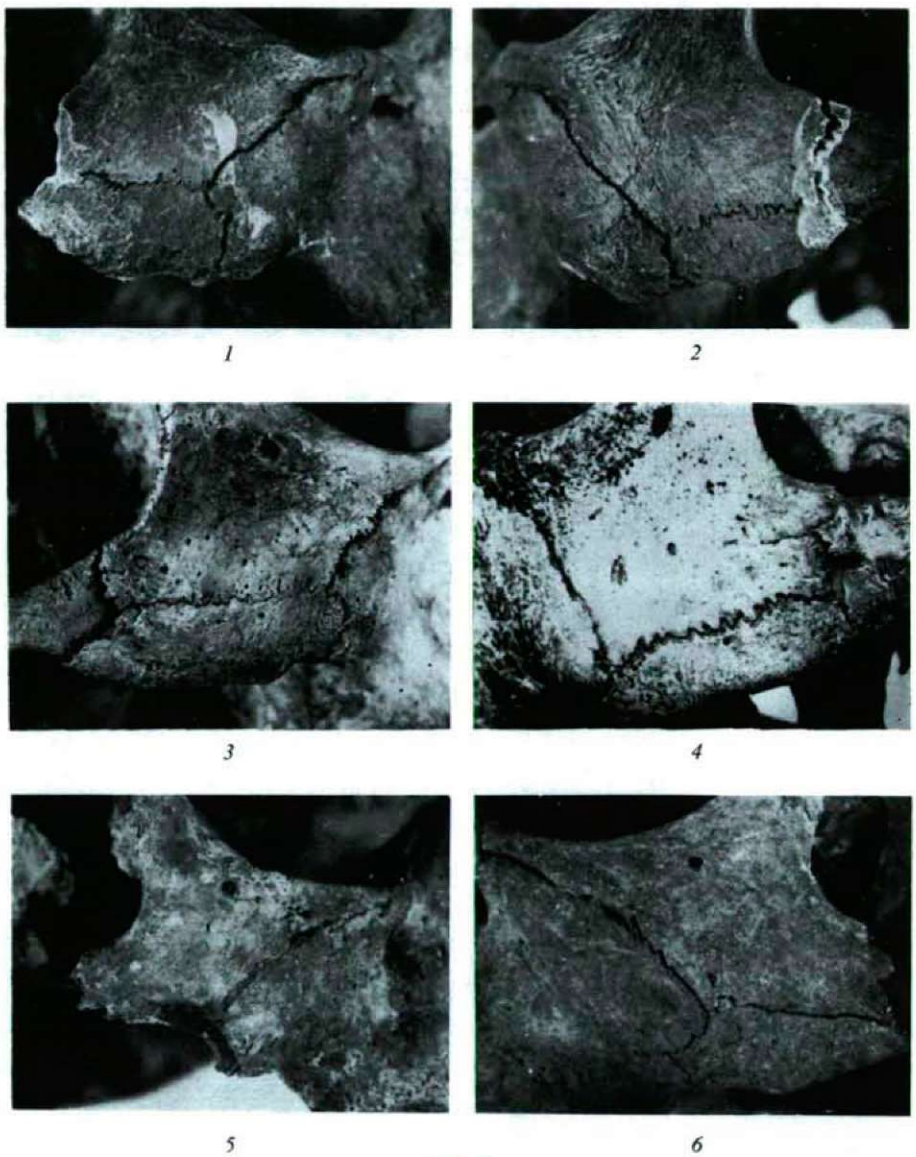


Fig. 3

6. Skull no. 1717. Site of find: Szeged-Fehértó "A" burial-ground, grave no. 61, Avar Period. A female of mature age. Ossified transverse suture on the right side (Fig. 2, 6), and os epiptericum on the right side. From a taxonomic viewpoint the find can not be evaluated (LIPTÁK and VÁMOS, 1969), but it can be stated that it is of a Europid character.

7. Skull no. 1804. Site of find: Szeged-Fehértó "A" burial-ground, grave no. 214, Avar Period. A female of mature age. Bilateral os malare bipartitum (Fig. 3, 1—2), with Worm-type bones in the lambdoid suture. The find primarily exhibist the features of the group of characteristics of the Pamirian race (LIPTÁK and VÁMOS, 1969).

8. Skull no. 864. Site of find: Szeged—Kundomb, grave no. 234, Avar Period. A female of adult age. Os malare bipartitum on the right side (Fig. 3, 3), with Worm-type bones in the lambdoid suture, and bilateral os epiptericum. From a taxonomic viewpoint the find primarily reveals the features of the Cromagnoid-B race (LIPTÁK and MARCSIK, 1966).

9. Skull no. 861. Site of find: Zenta—Farkas farm (Yugoslavia), grave no. 2, Arpadian age. The find is in the Vojvodanski Muzej, Novi Sad. A female of juvenile age. Os malare bipartitum on the left side (Fig. 3, 4), with Worm-type bones in the lambdoid suture. The find exhibits the characteristics of the Nordic race (BARTUCZ and FARKAS, 1958).

10. Skull no. 1175. Site of find: Kiszombor, grave no. 60/II, Gepid. The skull of a child of about six years (BARTUCZ, 1936), on which bilateral os malare bipartitum (Fig. 3, 5—6) can be observed. The right sutural bone is missing, but its position can be established unambiguously. As a result of the fragmentation of the find, the presence or absence of other anomalies can not be established.

Discussion

From among 1860 skulls in palaeoanthropological material randing in date from the Middle European Copper Age to the 17th century A.D., os malare bipartitum was observed in 10 cases (0.54%). It is striking that it occurred only in material from the Migration Period (1st millenium A.D.) and the Hungarian Middle Age. Its frequency appears very small compared to the literature data, and supports the observation that this is a rare anomaly.

The distribution of the ten cases with regard to sex and the side of the skull is as follows:

Side	Male	Female	Child	Total
Right	—	2	—	2
Left	2	1	—	3
Right and left	3	1	1	5
Total	5	4	1	10

In these ten cases the anomaly occurs more often in males and on both sides together, than in females and on only one side of the skull.

In 8 of the 10 cases some other anomaly too was present, which indicates the connection of this phenomenon with other variations. At any event, this appears to confirm that it may be related to the disturbance of the ossification centres.

It is obvious from the distribution according to sex and age that this is a congenital anomaly, which remains throughout the extrauterine life, while the obliteration of the suture takes place in a similar way as for other sutures of the skull. The transverse suture is generally finely serrated on the external surface, whereas its course on the inner surface is simple.

From a taxonomic viewpoint it is noteworthy that Mongolid or Mongoloid character could be observed in 3 of the 8 evaluable finds. Since the number of finds

possessing Mongolid or Mongoloid features among the 1860 skulls examined is relatively small, this suggests that the occurrence of os malare bipartitum is more frequent among the races of a Mongolid character than among the Europeans.

Since the observations do not differ essentially from the literature data, this anomaly can be regarded as being characteristic of the entire human race, but at the same time it is a very rare phenomenon.

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"SYMMETRICAL OSTEOPOROSIS" IN A PALAEOANTHROPOLOGICAL MATERIAL

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Abstract

The cause of "symmetrical osteoporosis", hyperostosis spongiosa cranii or porous hyperostosis (grave No. 299 from the cemetery at Kiszombor) is the hyperplasia of the red bony marrow, the development of which can be explained by hemolytic anemia, namely Cooley's anemia. In thalassemia, the X-ray picture of the cranium shows "bristling skull bones" or "hair standing on end". Thalassemia can not be established beyond doubt as the etiology of the bone deformation mentioned, as it is not possible to achieve the family reconstruction for the clarification of the clinical picture. Bearing in mind the corresponding literature data, therefore, iron deficiency anemia can be considered, too. The skull in grave 299 indicates that "symmetrical osteoporosis" is an unsuitable expression, hyperostosis spongiosa cranii being more correct.

Introduction

A localised deformation of Pre-Columbian Indian crania, in which the diploic substance appeared enlarged in the external parietal layer, was named "symmetrical osteoporosis" by HRDLIČKA (1914). The process begins in the orbital roof or in the frontal squama. In an extreme case, the appearance of the porous tissue may even result in a "coral"-form. The frequency of this deformity is higher in the coastal region than in the mountainous districts.

Other authors too, e.g. WILLIAMS (1929), HOOTON (1930) and WAKEFIELD—DELLINGER—CAMP (1937), mentioned symmetrical osteoporosis — as it was then named — of the crania of historical times.

Materials and Methods

The bone destruction described by these authors is shown by the cranium of an individual (Inf. II) from grave No. 299 in the cemetery at Kiszombor dating from the Migration Period. A detailed anthropological and pathological description of the cranium is to be found the book of BARTUCZ (1966). The main characteristics of its state are as follows:

1. In the parietal regions on both sides of the cranium, hyperplasia of the spongiosa with dendrite-shaped formations can be seen, encircling the area of the parietal tuber. That on the right is a little larger than that on the left (Fig. 1a, b, c).

2. In the upper medial parts of both orbitales tuberous protuberance is shown by the hyperplasia of the spongiosa, that in this case does not break through the external layer. According to NATHAN—HAAS (1966) this deformation is of trabecular type and corresponds to grade 6 (HENGEN 1972) (Fig. 2), established for the cribra orbitalia (WELCKER, 1888).

3. In the area above both mastoid processes, as well as in the alveolar and palatinal parts of the maxillary process and in the ala magna, small porosity can be observed.
4. Premature synostosis praecox.
3. The "hair on end" from (Fig. 3) is to be seen in the X-ray picture of the skull.

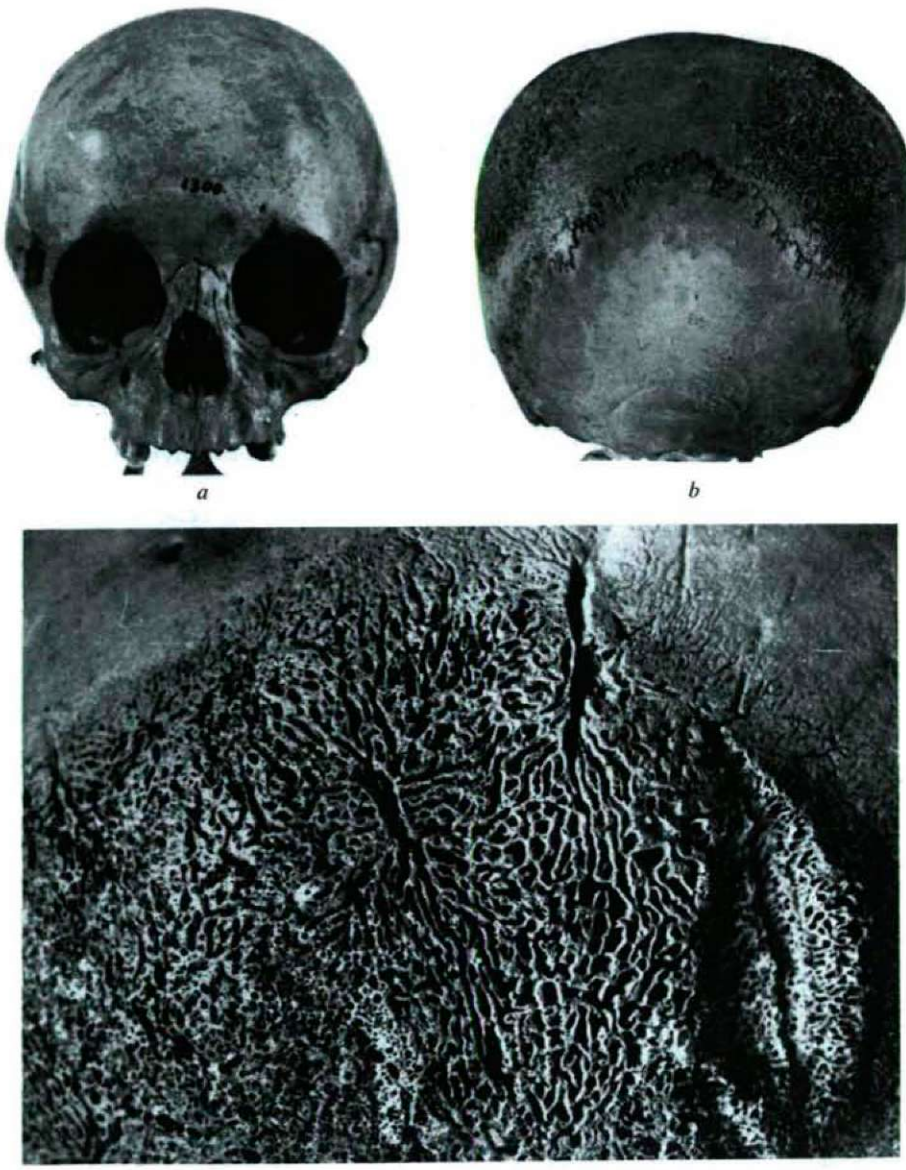

Fig. 1. Kiszombor, cemetery of the Migration Period grave 299 (1300).
a) Ventral aspect of skull.
b) Dorsal aspect of skull.
c) Hyperostosis spongiosa cranii.

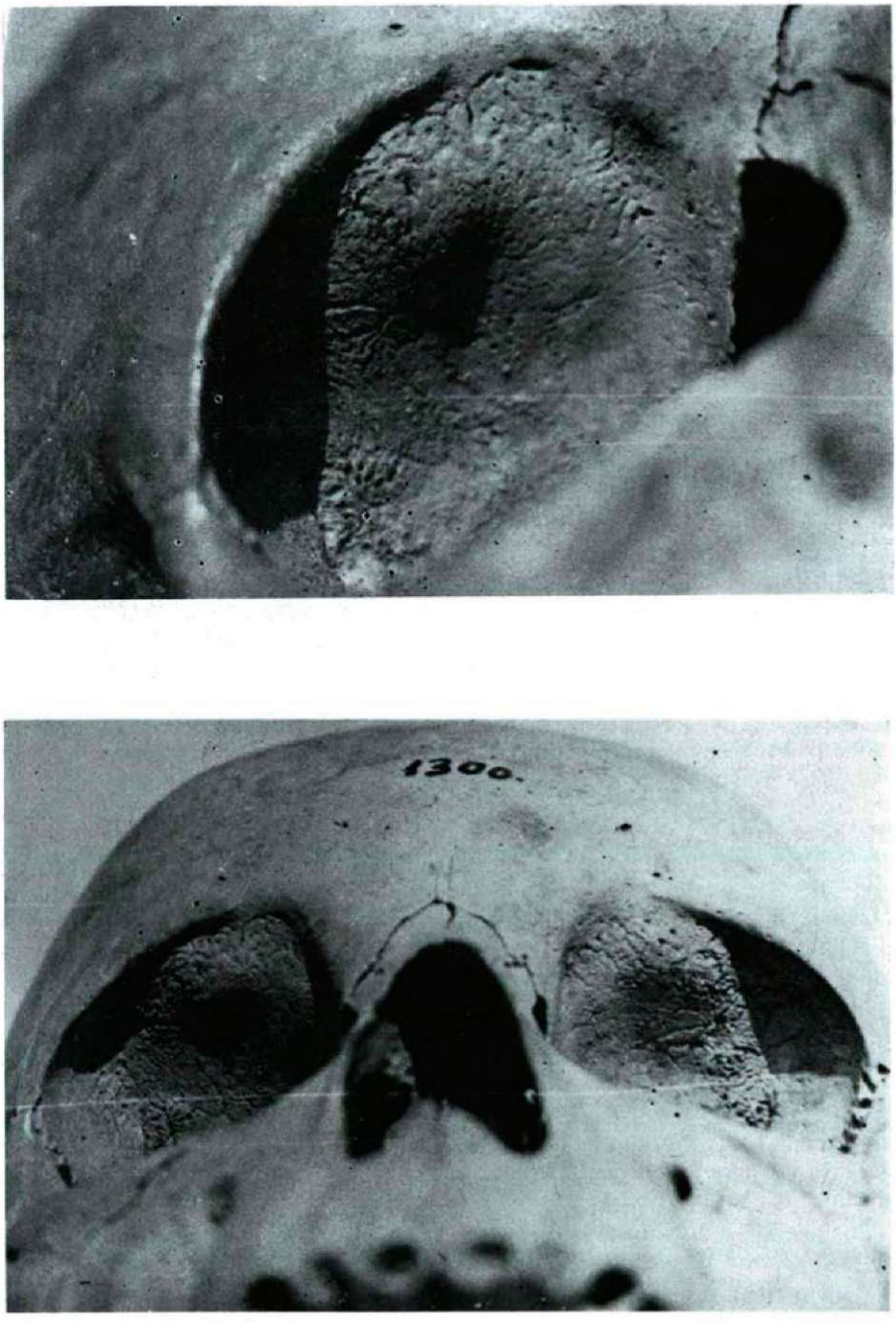

Fig. 2. Kiszombor, cemetery of the Migration Period grave 299 (1300).
Hyperostosis spongiosa orbitae (trabecular type).

Fig. 3. Kiszombor, cemetery of the Migration Period grave 299 (1300). Cranical X-ray pictures: "hair on end".

Discussion

The cause of "symmetrical osteoporosis", hyperostosis spongiosa cranii (HAMPERL—WEISS, 1955; MOSELEY, 1965) or porous hyperostosis (ANGEL, 1964; 1966) is the hyperplasia of the medulla, the development of which can be explained by hemolytic anemia, namely Cooley's anemia. Red marrow is situated in the lacunae of the spongiosa of the osteophyte, whereby new erythrogenic foci develop roughly compensating the severe anemia of the organism (HAMPERL—WEISS, 1955). In thalassemia, the X-ray picture of the cranium, "bristling skull bones", produced by bone trabecules pressed together, is very characteristic (VOGT—DIAMOND, 1930; CAFFEY, 1957). This severe cranial deformation is characteristic mainly of thalassemia major (Cooley's anemia). Apart from the widening of the diploic substance of the bones, the lowered pneumatisation of Highmore's antrum, and the hypertrophy of the upper part of the maxilla are well-known (POWELL—WEENS—WENGER, 1965). The X-ray picture can be characterised by a bone destruction similar to thalassemia major in every kind of congenital hemolytic anemia, thus in th. intermedia, th. minor, th. hemoglobin-S, th. hemoglobin-E; in every sort of sickle cell anemia; and in sphero- and elliptocytosis (MOSELEY, 1965).

In recent years, iron deficiency anemia turned out to give rise to the same skull defects as hemolytic anemia (MOSELEY, 1961; BURKO—MELLINS—WATSON, 1961; BRITTON—CANBY—KOHLER, 1960; SHAHIDI—DIAMOND, 1960; POWELL—WEENS—WENGER, 1965).

With regard to the X-ray picture of the cranium of a little girl suffering from severe anemia LIE (1958) states that the deformations are the same as those in Cooley's anemia. In this case, the anemia was the result of the multiplication of Ancylostoma duodenale.

The anemia-inducing effect of worms, particularly Ancylostoma duodenale and Diphyllobothrium latum, is well-known (HARANGHI, 1966).

Ancylostoma duodenale (Uncinaria) lives in the small intestine of the human, feeding on its mucous membrane and the blood of the vessels. One of its deleterious effects is thus to bring about loss of blood, while the penetration of its toxic dis-

charge into the blood causes serious complaints. Diphyllobothrium latum (wide tapeworm) is comparatively rare as a parasite of human (BREHM-revised by RAMMNER, 1960).

JELLIFFE and BLAKMAN (1962) give an account of the disease they named "Bahima". In this disease the X-ray picture of the cranium agrees with the well-known X-ray picture of hemolytic anemia, but the patients did not suffer from either thalassemia or sickle cell anemia or other hemolytic anemia. It was simply a question of iron deficiency anemia caused in the case of children by milk, their standing and main food.

In the establishment of the etiology of "symmetrical osteoporosis", the papers dealing with polycythemia must also be taken into consideration.

DYKSTRA—HALBERTSMA (1940) describe the thickening of the frontal region of the cranium in childhood.

CAFFEY (1961) reported on the connection with polycythemia in the case of cyanotic congenital heart diseases.

ASCENZI—MARINOZZI (1958) analyse the radiograms of the crania of patients suffering from this heart failure: a trabecular pattern with delimited fissures, and a parietal process, the bone marrow extending towards the periosteum.

The papers of MARIANI—BOSMAN (1962) and NICE—DAVIES—WOOD (1964) also report on bone deformations caused by the same disease.

The geographical localisation of the findspots of human skeletal remains originating from different historical ages and showing signs of porous hyperostosis exhibits a relation with the old-world occurrence of Plasmodium falciparium malariae, with the incidence of sickle cell anemia, and with iron deficiency anemia as one the results of protracted breast-feeding (MOSELEY, 1965).

From among the most important diseases characterised by erythroid hyperplasia in our case it is possible to exclude sickle cell anemia and its various forms, inherited sphero- and elliptocytosis (MOSELEY, 1965); the case of polyglobulia developing with cyanotic congenital heart diseases; and polycythemia vera rubra, or Osler—Vaquez disease (HARANGHI, 1966); but thalassemia and hypochromic anemia may be involved.

Thalassemia is a syndrome consisting of heterogeneous, hereditary anomalies, manifested in homozygotes in the form of severe anemia, but in heterozygotes only in formal anomalies of the erythrocytes. The two main clinicaly important types of the syndrome are alpha and beta thalassemia, depending on whether the formation of the alpha or beta chain of the globin component of the hemoglobin is retarded. In a heterozygote state (thalassemia minor) the hypochromic anemia develops only slowly, while in homozygotes (thalassemia major) a marked hypochromic anemia with anisocytosis and poikilocytosis can be observed. There is, also a transition between thalassemia major and thalassemia minor of course: thalassemia intermedia. Less known are alpha thalassemia and the HB LEPORE anomaly (MÁTYÁS, ref. 1973).

If some kind of thalassemia is considered, then in the case mentioned thalassemia major can come into question, as the roentgenogram of the cranium really corresponds to the bone deformity induced by this disease. At the same time, the localised osteoporous area observed in the cranium of several individuals of the series (os frontale facies orbitalis) would possibly correspond to other anomalies of thalassemia or to their early signs (CAFFEY, 1937; 1951). In this case, grave 299

would be (German/Gepid) rather, than one from the Arpad-Age (CSALLÁNY, 1961) although it is described by TÖRÖK (1936) as a grave without accessories.

Naturally, it is not possible to establish thalassemia beyond doubt as the etiology of the bone deformation mentioned, as it is not possible to achieve the family reconstruction for the clarification of the clinical picture. Bearing in mind the corresponding literature data, therefore, iron deficiency anemia too can be considered as a cause of the patho-morphological picture of the cranium, possibly in connection with helminthiasis.

"Symmetrical osteoporosis", introduced by HRDLIČKA as an anthropo-pathological term, is suggested by the skull in grave 299 to be a fairly unsuitable expression for the indicated pathological process. In fact, the above-mentioned expression hyperostosis spongiosa cranii is more correct.

(The author's thanks are due to Dr. L. PÁLDY — Roentg. Clinic, Szeged — who X-rayed the bones.)

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ANTHROPOLOGICAL ANALYSIS OF THE AVAR-PERIOD POPULATION OF SZEKSZÁRD—PALÁNKPUSZTA

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Abstract

In the vicinity of Szekszárd, at Palánkpuszta, between the years 1957 and 1960, there were excavated 233 graves from the Avar age. Out of them, the skeletal material of 136 graves could be rescued. The skeletal remains of 27 adult males and 37 females were suitable for being analysed in detail metrically, morphologically, and taxonomically. A result of the taxonomical analysis has been that the group of the brachycephals is together about 46 per cent of the total sample, that of the dolichocephals about 38 per cent. There could be demonstrated, anyway, in a less significant ratio, a Mongoloid racial component, as well. Taking into consideration the archaeological investigations of ÁGNES SALAMON, there were characteristic of the early period of the cemetery the dolicocephalic and Mongoloid components, while of the later period the brachycephals.

In the vicinity of Szekszárd, at Palánk-puszta, on a lofty sand-hill salvaging excavations were carried out between 1957 and 1960, directed in the first excavation period by archaeologist GY. KISS and in the later years by archaeologist ÁGNES SALAMON. P. LIPTÁK joined in the excavations, as well (with some interruptions). The plan of a part of the cemetery is, unfortunately, not available. The excavation is but partial; the tempo and direction of the excavation were determined by the points of view of rescue. In the area of the Avar-period cemetery there was found also a Hun-age cemetery from the 5th century, containing artificially deformed crania. In the course of the excavation there were found 233 numbered graves altogether. In some cases, in the absence of the archaeologist directing the excavation, the rescue was carried out by the Museum of Szekszárd; the graves have sometimes got a different numbering or got into the Museum as scattered items. Only the preliminary elaboration of the archaeological finds has taken place (SALAMON, 1968). The history of excavation can be followed in the corresponding volumes of the Archaeológiai Értesítő 1958, 1959, 1960, 1961). The skeletal material of graves 234 to 261 could no more be investigated here, in this paper.

ÁGNES SALAMON's comments on the archaeological finds will be published separately.

From the Avar-age cemetery of Szekszárd—Palánk there could be rescued the skeletal remains of 136 graves altogether (Table 1). The state of preservation of the material is beneath the average. The number of fragmentary crania is 38 and in 19 cases there were salvaged only postcranial skeletons. The number of adult and subadult skeletons in good state of preservation is 79. The number of adult crania suitable for detailed metrical analysis is unfortunately low, as compared to the high grave number of the excavation, namely 27 males and 37 females. The considerable female majority came about obviously casually as the excavation

Table 1. Szekszárd—Palánk, avar period: Skeletal material

Characterization of the material		Inf. I.	Inf. II.	Juv.	Ad.	Mat.	Sen.	Total
Fragmentary crania (unmeasured)	Males	—	—	—	4	10	2	16 (42%)
	Females	—	—	—	7	5	—	12 (32%)
	Undeterminable	3	2	3	2	—	—	10 (26%)
	Total:	3	2	3	13	15	2	38
Postcranial skeletons	Males	—	—	1	—	5	—	6 (32%)
	Females	—	—	—	1	5	—	6 (32%)
	Undeterminable	—	1	2	—	4	—	7 (36)%)
	Total:	—	1	3	1	14	—	19
Well preserved crania (measured)	Males	—	—	—	10	16	1	27 (34%)
	Females	—	—	1	24	9	4	38 (48%)
	Undeterminable	2	7	5	—	—	—	14 (18%)
	Total:	2	7	6	34	25	5	79
	Sum-total:	5 (3,7%)	10 (7,3%)	12 (8,9%)	48 (35,3%)	54 (39,7%)	7 (5,1%)	136

Table 2. Szekszárd—Palánk, avar period

No. of measurements (Martin)	Measurements and indices	Males				Females			
		N	V	M	s	N	V	M	s
1.	Glabello-occipital length	21	175—200	184,1	6,18	34	163—183	174,2	4,18
8.	Maximum breadth of cranium	22	128—162	146,1	7,96	35	128—151	141,0	5,84
9.	Minimum frontal breadth	25	89—109	99,3	4,22	35	89—104	95,8	4,03
17.	Basion-bregma height	14	131—144	137,1	3,58	22	118—140	130,3	4,96
38.	Cranial capacity	12	1340—1660	1561,8	101,20	17	1120—1450	1323,8	98,20
45.	Bizygomatic breadth	17	121—147	134,7	6,58	22	118—139	126,7	5,02
47.	Face height	13	106—131	119,6	7,68	23	101—119	110,6	4,71
48.	Upper face height	22	58—81	70,7	5,56	30	58—75	67,1	4,21
72.	Total facial angle	14	77°—91°	83,6	4,86	13	81°—90°	85,6	2,39
8:1	Cranial index	18	68—91	79,3	5,86	30	72—89	81,3	4,66
17:1	Length-height index	12	70—79	74,3	2,89	17	69—82	74,8	3,05
17:8	Breadth-height index	14	80—101	94,2	5,96	20	84—98	93,7	3,96
9:8	Fronto-parietal index	20	61—75	67,3	4,16	30	62—74	68,1	2,86
47:45	Facial index	10	82—97	87,5	4,61	16	82—99	88,1	4,76
48:45	Upper facial index	15	47—57	52,3	3,12	19	46—62	53,9	4,31
52:51	Orbital index	23	70—92	81,8	5,14	28	80—100	87,4	5,51
54:55	Nasal index	19	36—65	49,8	6,18	26	39—59	49,3	4,72
	Calculated stature	27	160—176	167,0	3,97	34	146—165	155,5	4,14

Table 3. Szekszárd—Palánk avar period
Distribution of the principal metrical characters

Characters			Males	Females	Total
8:1 Cranial index	Dolichokranic	70—74,9	3 (17%)	4 (13%)	7 (15%)
	Mesokranic	75—79,9	6 (33%)	8 (27%)	14 (29%)
	Brachykranic	80—84,9	5 (28%)	10 (33%)	15 (31%)
	Hyperbrachykranic	85—89,9	3 (16%)	8 (27%)	11 (23%)
	Ultrabrachykranic	90—x	1 (6%)	—	1 (2%)
		Total:	18	30	48
17:1 Length-height index	Chamaekranic	x—69,9	—	1 (6%)	1 (3%)
	Orthokranic	70—74,9	7 (58%)	9 (53%)	16 (55%)
	Hypsikranic	75—x	5 (42%)	7 (41%)	12 (41%)
		Total:	12	17	29
17:8 Breadth-height index	Tapeinokranic	x—91,9	4 (29%)	7 (35%)	11 (32%)
	Metriokranic	92—97,9	8 (57%)	12 (60%)	20 (59%)
	Akrokranic	98—x	2 (14%)	1 (5%)	3 (9%)
		Total:	14	20	34
9:8 Fronto-parietal index	Stenometopic	x—65,9	7 (35%)	5 (17%)	12 (24%)
	Metriometopic	66—68,9	2 (10%)	11 (37%)	13 (26%)
	Eurymetopic	69—x	11 (55%)	14 (46%)	25 (50%)
		Total:	20	30	50
47:45 Facial index	Euryprosopic	80—84,9	2 (20%)	4 (25%)	6 (23%)
	Mesoprosopic	85—89,9	5 (50%)	6 (38%)	11 (42%)
	Leptoprosopic	90—94,9	2 (20%)	5 (31%)	7 (27%)
	Hyperleptoprosopic	95—x	1 (10%)	1 (6%)	2 (8%)
		Total:	10	16	26
48:45 Upper facial index	Euryene	45—49,9	3 (20%)	4 (21%)	7 (21%)
	Mesene	50—54,9	7 (47%)	7 (37%)	14 (41%)
	Leptene	55—59,9	5 (33%)	7 (37%)	12 (35%)
	Hyperleptene	60—x	—	1 (5%)	1 (3%)
		Total:	15	19	34
52:51 Orbital index	Chamaekonch	x—75,9	2 (9%)	—	2 (4%)
	Mesokonch	76—84,9	14 (61%)	12 (43%)	26 (51%)
	Hypsikonch	85—x	7 (30%)	16 (57%)	23 (45%)
		Total:	23	28	51
54:55 Nasal index	Leptorrhine	x—46,9	4 (21%)	7 (27%)	11 (24%)
	Mesorrhine	47—50,9	9 (47%)	8 (31%)	17 (38%)
	Chamaerrhine	51—57,9	4 (21%)	10 (38%)	14 (31%)
	Hyperchamaerrhine	58—x	2 (11%)	1 (4%)	3 (7%)
		Total:	19	26	45
38 Cranial capacity		Males / Females			
	Oligencephalic	x—1300 / x—1150	—	2 (12%)	2 (7%)
	Euencephalic	1301—1450 / 1151—1300	3 (25%)	3 (18%)	6 (21%)
	Aristencephalic	1451—x / 1301—x	9 (75%)	12 (70%)	21 (72%)
		Total:	12	17	29

Table 3

Characters			Males	Females	Total
72 Total angle facial	Prognathous.....	70°—79°	4 (29%)	—	4 (15%)
	Mesognathous	80°—84°	4 (29%)	5 (38%)	9 (33%)
	Orthognathous	85°—92°	6 (42%)	8 (62%)	14 (52%)
		Total:	14	13	27
		Males / Females			
Calculated stature	Short.....	150—159,9 / 140—148,9	—	2 (6%)	2 (3%)
	Short medium...	160—163,9 / 149—152,9	6 (22%)	4 (12%)	10 (16%)
	Medium ...	164—166,9 / 153—155,9	6 (22%)	13 (38%)	19 (31%)
	Tall medium	167—169,9 / 156—158,9	8 (30%)	6 (18%)	14 (23%)
	Tall	170—179,9 / 159—167,9	7 (26%)	9 (26%)	16 (26%)
		Total:	27	34	61

was carried out not in a continuous area and, what is more, the uncovered territory is only a part of the cemetery.

The most important parameters are contained in Table 2 and the distribution of the main metric characters in Table 3. The individual metric data of males and females are to be found as an appendix to the paper. The enumeration of the rather numerous fragmentary material is omitted.

The *general characterisation of the series* is given on the basis of males. The cranium is of medium length, medium breadth, the mean of cranial index is approaching the upper limit of mesocrany. On the basis of index categories we can speak of some predominance of mesocrany and brachycrany. The cranium is higher than medium-sized, ortho-hypsicranic, resp. metriocranic. In vertical norm the cranial contour is highly various, with slight preponderance of the ovoid form. The forehead is of medium breadth, as to the transversal-frontoparietal index, the males are in two groups: the stenometopic and eurymetopic ones. The glabella is of 2 to 4 degree (Broca). The value of cranial capacity is, owing to the low case-number, better to be disregarded. The zygomatic arch is of medium breadth, the upper face is of medium height and on the basis of upper-face index mesene. Mesoconchy and mesorrhiny occur very often. The mean value of the facial profile falls to the category of mesognathia but prognathic and orthognathic facial profiles are to be found, as well. The mean of the calculated stature is at the border of medium and tall medium; the most frequent categories are the tall medium and tall stature.

With regard to the higher frequencies, the general characteristics of the females of the sample is more reliable. The cranium is of medium length, of medium breadth. On the basis of the mean of cranial index they are mesocranic; on the basis of index categories the relative preponderance of brachycrany is characteristic. The cranium is higher than medium, being ortho-hypsicranic, resp. metriocranic. With regard to the vertical cranial contour, the firm prevalence of the sphenoid form is characteristic. The forehead is of medium breadth. On the basis of the transversal-frontoparietal index it is metrio-eurymetopic. The glabella is mostly of 1 to 2 degrees (Broca). The cranial capacity is, on the basis of the mean, bigger than medium-sized, aristencephaly is prevalent. The face is of medium breadth, medium height, meso-

leptoprosopic, resp. mesene-leptene. The orbits are, in case of females, considerably high, being prevalently hypsiconchic. In respect of the nasal index, they are more often meso-chamaerrhine. The fossa canina agrees with that of males. The facial profile, established in a comparatively low number of cases, is meso-orthognathous. A medium alveolar prognathism is characteristic. The stature is very variable, the most frequent one being the middle-sized and tall stature category.

Table 4. Szekszárd—Palánk, avar period

Taxonomic analysis		Males	Females	Total
Brachycephals	Undetermined (br)	4	9	13 (27%)
	Pamirian (p)	1	5	6 (13%)
	Alpine, Lappid (a, l)	—	3	3 (6%)
	Sum-total:	5	17	22 (46%)
Nordic, Atlanto-Mediterranean (n)		7	5	12 (25%)
Gracile-Mediterranean (m)		2	4	6 (13%)
Cromagnoids (crA, crB)		3	1	4 (8%)
Turano-Mongoloids (t, moid)		1	3	4 (8%)
	Total:	18	30	48

The result of *taxonomic analysis* is contained in Table 4. The group of Brachycephals (br) amounts together to 46 per cent of the whole series. An undeterminable brachycephalic component prevails, and in addition to that, there can be established Pamirian, Alpine and Lappid elements. In case of females, the Brachycephals are expressly predominating. The Nordoid, that is to say Nordic-Atlantomediterranean (n) taxon is giving together 25 per cent of the series. In case of males, its percentage is more considerable. The gracile Mediterranean (m) race can be demonstrated, too, as a rather considerable component. — Besides the above-mentioned taxons, the Cromagnoids as well as the Turanids and on — in detail not determinable — Mongoloid component can be diagnosed in this series.

It was suitable, to compare the taxonomical analysis — carried out in adult crania of good state of preservation — with the archaeological results. At my request, ÁGNES SALAMON has elaborated the archaeological groups resp. periods, according to graves, established on the basis of her detailed archaeological study, to be published at a future date. The males belonging to the first period are characterized by a stamped plate girdle set; the most numerous is the second or middle group, characterized — together with the third group — by a cast girdle set (griffin and tendril group). As the number of adult skeletons in a good state of preservation is comparatively not high, and as there were graves without any archaeological grave goods or at least without significant ones, the following results have developed for information:

a) the dolichocephals of tall stature are characteristic of the early (stamped plate girdle set) group, and there could be found some individuals showing Mongoloid features, as well, only in that group;

b) the brachycephalic components, among them the representatives of the Pamirian race are first of all characteristic of the "griffin and tendril" group.

Table 5. Szekszárd—Palánk, avar-period: Males (1)

No. of measure-ments (Martin)	Measurements and indices	1. 10 212 Mat.	2. 10 213 Juv-Ad.	(11.) 10 216 Ad.	12. 10 218 Ad.	21. 10 222 Ad.	29. 10 225 Mat.	38. 10 232 Mat.	70. 10 354 Mat.	78. 10 358 Mat.
1.	Glabello-occipital length	181	180	—	—	200	193	178	(175)	—
1c.	Metopium occipital length		178	180	—	—	191	188	176	173
5.	Basion-nasion length	—	100	—	—	111	107	104	—	—
8.	Maximum breadth of cranium	146	137	—	—	142	141	162	—	—
9.	Minimum frontal breadth	101	96	98	101	102	106	102	102	97
17.	Basion-bregma height	—	132	—	—	142	137	131	—	—
20.	Porion bregma height	116	111	—	—	115	112	111	—	—
32/1-a.	Frontal angle	47°	48°	—	—	45°	45°	43°	—	—
38.	Cranial capacity	—	1340	—	—	1586	1500	1590	—	—
40.	Sup. facial length	—	92	—	—	111	107	108	—	—
45.	Bizygomatic breadth	(130)	125	—	—	141	142	144	—	—
46.	Maxillar breadth	95	95	—	100	96	—	96	—	92
47.	Total facial height	—	107	131	—	120	—	—	—	116
48.	Upper facial height	67	69	80	67	74	81	75	69	69
51.	Orbital breadth	38	37	38	40	39	42	41	41	39
52.	Orbital height	31	32	35	31	32	35	36	33	35
54.	Nasal breadth	—	—	21	24	24	27	26	25	25
55.	Nasal height	51	48	57	45	52	54	54	47	50
62.	Palatal length	45	—	—	48	57	49	53	—	49
63.	Palatal breadth	—	37	—	46	44	—	—	—	43
65.	Bicondylar-diameter	—	112	—	—	(121)	—	—	—	—
66.	Bigonial-diameter	—	95	—	—	107	—	(108)	—	—
69.	Mental height	(25)	32	38	—	35	—	(32)	—	32
70.	Ramus height	68	57	—	—	76	—	75	—	—
71.	Ramus breadth	—	34	35	—	35	—	34	—	30
72.	Total facial angle	84°	89°	—	—	78°	78°	77°	—	—
8:1	Cranial index	80,7	76,1	—	—	71,0	73,1	91,0	—	—
17:1	Length-height index	—	73,3	—	—	71,0	71,0	73,6	—	—
17:8	Breadth-height index	—	96,4	—	—	100,0	97,2	80,9	—	—
9:8	Transvers. frontopar. index	69,2	70,1	—	—	71,8	75,2	62,9	—	—
47:45	Facial index	—	85,6	—	—	85,1	—	—	—	—
48:45	Upper facial index	51,5	55,2	—	—	52,5	57,0	52,1	—	—
52:51	Orbital index	81,6	86,5	92,1	77,5	82,1	83,3	87,8	80,5	89,7
54:55	Nasal index	—	—	36,8	53,3	46,2	50,0	48,2	53,2	50,0
63:62	Palatal index	—	—	—	95,8	77,2	—	—	—	87,8
Norma verticalis		Ovoid	Pent.	Ovoid	—	Ell.	Ell.	Szfer.	Szfer.	—
Glabella		1	1	2	2—3	3	3	2	2	2
Protuberantia occipitalis externa		2	0	0	1	0	1	0	1	—
Fossa cania		2	2	1	3	2	2	4	4	2
Spina nasalis anterior		2	2	2	2	1	3	3	1	4
Alveolar prognathism		3	1	1	2	2	1	2	2	3
Calculated stature		—	166	165	—	—	—	170	169	167
Taxon		br	—	—	crB	—	n—x	p	—	n—x

Table 5. Szekszárd—Palánk, avar period: Males (2)

No. of measurements (MARTIN)	99. 10 369 Mat	106. 10 373 Ad.	(124.) 10 380 Mat.	136. 10 392 Ad.	139. 10 395 Ad.	155. 10 399 Mat.	— 10 410 Ad.	— 10 414 Mat.	— 10 415 Mat.	176. 10 417 Mat.	181. 10 419 Mat.
1.	176	178	180	180	183	(193)	—	—	179	185	—
1c.	174	178	177	168	174	—	172	178	174	182	—
5.	105	103	99	—	109	110	99	98	97	(105)	—
8.	148	155	140	155	142	—	136	148	151	158	155
9.	93	97	98	96	89	99	—	103	96	105	109
17.	136	(142)	137	—	136	—	138	137	140	(136)	—
20.	109	—	117	—	112	—	111	118	—	—	—
32/1-a.	45°	—	52°	49°	52°	—	54°	56°	—	—	—
38.	1489	(1647)	1423	—	1396	—	—	—	1553	(1657)	—
40.	98	—	102	—	(107)	105	95	91	—	—	—
45.	135	—	135	147	133	—	129	130	—	—	—
46.	103	—	102	108	99	99	94	101	—	99	—
47.	115	—	124	124	114	125	106	—	—	—	—
48.	69	—	75	72	63	78	65	70	—	66	(68)
51.	40	33	40	39	39	44	39	45	—	42	40
52.	32	30	35	34	31	32	30	—	—	33	33
54.	27	—	25	28	26	26	26	25	—	—	26
55.	45	—	50	45	—	52	46	—	—	—	—
62.	53	—	52	55	52	55	48	48	—	52	52
63.	—	—	44	44	41	42	40	—	—	—	—
65.	—	—	123	136	126	—	109	—	—	—	—
66.	—	104	101	115	108	111	107	—	—	101	—
69.	(29)	38	40	34	32	39	29	—	—	(26)	—
70.	—	65	72	63	75	70	75	—	—	62	—
71.	—	27	35	32	33	33	32	—	—	32	33
72.	85°	—	81°	89°	81°	—	80°	(90°)	—	—	—
8:1	84,1	87,1	77,8	86,1	77,6	—	—	—	84,4	85,4	—
17:1	77,3	79,8	76,1	—	73,8	—	—	—	78,2	73,5	—
17:8	91,9	91,6	97,9	—	95,1	—	101,5	92,6	92,7	86,1	—
9:8	62,8	62,6	70,0	61,9	62,7	—	—	69,6	63,6	66,5	70,3
47:45	85,2	—	91,9	84,4	85,7	—	82,2	—	—	—	—
48:45	51,1	—	55,6	49,0	47,4	—	50,4	53,9	—	—	—
52:51	80,0	90,9	87,5	87,2	79,5	72,7	76,9	—	—	78,6	82,5
54:55	50,9	—	48,1	50,9	59,6	47,3	54.2	52,1	—	—	50,0
63:62	—	—	88,0	97,8	—	80,8	86,9	—	—	—	—
Norma verticalis	Pent.	Szfer.	Ell.	Szfer.	Ovoid	Ovoid	Pent.	Szfen.	Ovoid	Pent.	Szfer.
Glabella	3	4	4—5	3	4	4	4	—	5	2	3
Prot. occ. ext.	2	0	2	0	0	—	1	3	1	0	—
Fossa canina	3	—	5	1	2	3	3	3	—	4	2
Spina nas. ant.	2	—	4	2	1	1	2	—	—	1	1
Alv. prognathism	3	—	2	2	2	2	2	1	—	2	2
Termet	166	160	—	—	—	166	—	—	—	—	—
Taxon	br—x	—	m—n	t—x	(?)-moid	n	m—cr	—	br	crB	—

Table 5. Szekszárd—Palánk, avar period: Males (3)

No. of measurements (MARTIN)	188/2. 10 425 Ad.	195. 10 429 Mat.	209. 11 642 Sen.	211. 11 644 Ad.	213. 11 645 Mat.	225. 11 653 Mat.
1.	187	183	186	186	190	187
1c.	191	177	179	186	185	183
5.	—	105	—	(110)	—	105
8.	128	140	150	149	145	141
9.	95	98	96	101	102	99
17.	—	—	—	144	—	132
20.	117	—	—	119	—	118
32/1-a.	52°	—	—	49°	—	48°
38.	—	—	—	1660	—	1595
40.	—	95	—	(95)	—	93
45.	121	131	(133)	(133)	141	135
46.	90	94	—	97	—	99
47.	—	115	—	126	—	131
48.	58	70	—	75	—	(77)
51.	41	43	—	46	42	45
52.	29	33	(34)	36	35	38
54.	28	25	—	23	—	24
55.	43	50	—	59	—	55
62.	—	—	—	—	—	(55)
63.	—	40	—	40	—	—
65.	—	—	—	125	—	119
66.	—	—	—	103	—	108
69.	—	—	—	(35)	—	35
70.	—	70	—	72	—	67
71.	—	32	—	32	—	28
72.	79°	—	—	88°	—	(91°)
8:1	68,5	76,5	80,7	80,1	76,3	75,4
17:1	—	—	—	77,4	—	70,6
17:8	—	—	—	96,6	—	93,6
9:8	74,2	70,0	64,0	67,8	70,3	70,2
47:45	—	87,8	—	(94,7)	—	97,0
48:45	47,9	53,4	—	(56,4)	—	(57,0)
52:51	70,7	76,7	—	78,3	83,3	84,4
54:55	65,1	50,0	—	39,0	—	43,6
63:62	—	—	—	—	—	—
Norma verticalis	Ell.	Ovoid	Szphen.	Szphen.	Szphen.	Ovoid
Glabella	2	3	2	3	2	2
Prot. occ. ext.	0	1	0	0	—	1
Fossa canina	4	2	3	2	3	3
Spina nas. ant.	1	2	—	2	2	—
Av. prognathism	3	2	—	1	2	—
Stature	—	173	162	169	176	170
Taxon	crA—x	n—x	—	br—x	n—x	n

Table 6. Szekszárd—Palánk, avar period: Females (1)

No. of measurements (MARTIN)	Measurements and indices	(13.) 10 219 Mat.	15. 12 220 Ad.	20. 10 221 Ad.	30. 10 226 Ad.	32. 10 228 Ad.	37. 10 231 Mat-Sen.	44. 10 235 Ad.	45. 10 236 Ad.	49. 10 353 Ad.
1.	Glabello-occipital length	—	175	(181)	168	171	173	169	—	179
1c.	Metopion-occipital length	173	173	—	165	171	175	164	—	180
5.	Basion-nasion length	93	—	—	97	91	97	100	92	97
8.	Maximum breadth of cranium	140	144	140	140	131	141	132	140	140
9.	Minimum frontal breadth	98	101	—	96	93	99	92	98	94
17.	Basion-bregmaheight	130	—	—	128	128	127	124	130	134
20.	Porion bregma height	112	—	—	111	109	113	—	111	—
32/1-a.	Frontal angle	48°	—	—	48°	52°	49°	—	43°	—
38.	Cranial capacity	1326	—	—	1240	1171	1326	1134	—	1423
40.	Sup. facial length	(86)	—	—	98	84	92	—	90	—
45.	Bizygomatic breadth	130	—	—	—	122	128	—	118	—
46.	Maxillar breadth	95	92	89	96	91	88	—	90	—
47.	Total facial height	—	—	—	115	114	109	—	101	—
48.	Upper facial height	—	68	—	73	67	67	—	58	62
51.	Orbital breadth	38	39	37	39	36	40	—	37	37
52.	Orbital height	31	35	34	36	33	32	—	33	31
54.	Nasal breadth	(26)	24	25	24	26	25	—	22	—
55.	Nasal height	49	49	—	51	57	48	—	39	—
62.	Palatal length	—	45	—	44	42	44	—	—	—
63.	Palatal breadth	44	37	39	41	—	38	—	40	44
65.	Bicondylar-diameter	—	—	—	116	112	—	—	110	—
66.	Bigonial-diameter	—	—	—	98	—	—	—	92	(95)
69.	Mental height	—	—	(33)	33	29	30	28	27	29
70.	Ramus height	—	—	63	61	67	—	52	65	—
71.	Ramus breadth	—	—	35	34	27	27	28	30	31
72.	Total facial angle	88°	—	—	81°	85°	85°	—	83°	—
8:1	Cranial index	—	82,3	77,4	83,3	76,6	81,5	78,1	—	78,2
17:1	Length-height index	—	—	—	76,2	74,9	73,4	73,4	—	74,9
17:8	Breadth-height index	92,9	—	—	91,4	97,7	90,1	93,9	92,9	95,7
9:8	Transvers. . frontopar. index	70,0	70,1	—	68,6	71,0	70,2	69,7	70,0	67,1
47:45	Facial index	—	—	—	—	93,4	85,2	—	85,6	—
48:45	Upper facial index	—	—	—	—	54,9	52,3	—	49,2	—
52:51	Orbital index	81,6	89,7	91,9	92,3	91,7	80,0	—	89,2	83,8
54:55	Nasal index	53,1	49,0	—	47,1	45,6	52,1	—	56,4	—
63:62	Palatal index	—	82,2	—	93,2	—	86,4	—	—	—
Norma verticalis		Ovoid	Pent.	Ell.	Szfer.	Szfen.	Ovoid	Pent.	Szfen.	Ell.
Glabella		1	2	—	1	1	1	2	1	2
Protuberantia occipitalis externa		0	0	0	0	0	0	0	0	1
Fossa canina		1	3	3	2	2	3	—	3	2
Spina nasalis anterior		—	1	1	3	1	2	—	—	1
Alveolar prognathism		1	2	3	2	1	2	2	2	3
Calculated stature		—	—	—	153	155	155	151	—	153
Taxon		moid	(br(p)	—	br(p)	n	br—x	—	br	crA

Table 6. Szekszárd—Palánk, avar period: Females (2)

No. of measurements (MARTIN)	73. 10 355 Ad.	74. 10 356 Ad.	86. 10 362 Mat.	95. 10 366 Mat.	97. 10 367 Ad.	98. 10 368 Mat.	125. 10 382 Ad.	134. 10 390 Mat.	137. 10 393 Ad.	146. 10 397 Mat.	158. 10 400 Ad.
1.	171	174	166	181	—	169	179	174	170	175	—
1c.	164	171	164	184	—	169	177	170	164	174	—
5.	(91)	101	—	—	99	100	96	101	100	—	—
8.	136	141	129	134	141	—	(135)	146	145	128	—
9.	89	94	93	93	92	90	93	102	97	95	96
17.	(118)	131	—	—	139	129	128	133	140	—	—
20.	—	108	—	—	—	—	—	111	121	109	—
32/1-a.	—	44°	—	—	—	—	—	46°	51°	46°	—
38.	(1120)	1326	—	—	—	—	(1258)	1409	1409	—	—
40.	(92)	95	—	—	93	96	91	96	98	—	—
45.	123	128	121	(118)	(123)	—	—	129	128	123	—
46.	91	93	82	92	88	87	89	92	95	—	—
47.	103	109	111	(117)	115	104	—	114	117	—	—
48.	65	68	67	73	73	67	(61)	75	69	69	68
51.	37	—	35	40	38	38	37	39	39	39	38
52.	33	32	34	33	38	33	30	36	33	33	34
54.	23	24	24	24	24	24	25	25	25	22	—
55.	48	48	50	51	52	45	42	57	47	52	51
62.	44	44	—	—	43	42	43	45	44	—	—
63.	36	44	—	—	42	35	—	40	42	—	—
65.	(113)	—	—	—	112	117	—	115	111	126	—
66.	(88)	—	—	(91)	96	91	—	101	94	—	—
69.	25	32	—	39	29	32	—	32	32	27	—
70.	58	62	66	58	66	59	—	65	71	64	—
71.	30	32	26	30	28	30	—	28	34	29	—
72.	—	84°	—	—	—	—	—	83°	84°	88°	—
8:1	79,5	81,0	77,7	74,0	—	—	75,4	83,9	85,3	73,1	—
17:1	69,0	77,0	—	—	—	76,3	71,5	76,4	82,4	—	—
17:8	86,8	92,9	—	—	98,6	—	94,8	91.1	96,6	—	—
9:8	65,4	66,7	72,1	69,4	65,3	—	68,9	69,9	66,9	74,2	—
47:45	83,7	85,3	91,7	99,2	93,5	—	—	88,4	91,4	—	—
48:45	52,8	53,1	55,4	62,4	59,4	—	—	58,1	53,9	56,1	—
52:51	89,2	—	97,1	82,5	100,0	86,8	81,1	92,3	84,6	84,6	89,5
54:55	47,9	50,0	48,0	47,1	46,2	53,3	59,5	43,9	53,2	42,3	—
63:62	81,8	100,0	—	—	97,7	83,3	—	88,9	95,5	—	—
Norma verticalis	Szfen.	Szfer.	Szfen.	Pent.	Ell.	Szfen.	Ovoid	Pent.	Szfen.	Ell.	—
Glabella	2	1	1	1—2	2	1	3	1	2	2	1
Prot. occ. ext.	0	0	1	1	—	0	0	0	0	1	—
Fossa canina	3	2	3	4	3	2	3	2	1	1	2
Spina nas. ant.	1	2	—	3	1	1	2	1	4	2	1
Alv. prognathism	2	2	2	2	2	2	2	2	2	2	3
Calculated stature	—	157	—	—	154	159	150	158	155	154	—
Taxon	m—x	br—x	m—x	n	br(?)	n—x	m—x	t	p	m	(moid)

Table 6. Szekszárd—Palánk, avar period: Females (3)

No. of measurements (MARTIN)	166. 10 405 Ad.	167. 10 406 Juv-Ad.	I. 10 237 Ad.	5. 10 409 Sen.	— 10 411 Ad.	177. 10 418 Mat.	180. 10 435 Ad.	183. 10 421 Ad.	184. 10 422 Ad.	188/1. 10 437 Mat.	192. 10 438 Ad.
1.	182	—	170	172	175	166	179	183	—	182	177
1c.	181	—	169	173	173	—	177	182	—	182	173
5.	—	—	99	104	103	(92)	—	101	—	—	—
8.	—	—	139	147	140	(142)	151	136	—	141	146
9.	—	95	92	95	100	—	94	97	89	104	100
17.	—	125	136	134	131	—	—	133	—	—	—
20.	—	—	110	113	115	—	—	—	—	—	111
32/1-a.	—	—	44°	51°	50°	—	—	—	—	—	53°
38.	—	—	1335	1453	1335	—	—	1359	—	—	—
40.	—	—	88	—	96	—	—	90	—	—	—
45.	—	(128)	123	135	—	—	—	(127)	—	—	128
46.	90	92	85	109	—	102	—	92	86	—	94
47.	(112)	113	105	—	115	112	—	105	107	—	119
48.	70	72	70	—	70	—	—	62	64	—	69
51.	—	40	38	38	40	38	—	—	—	—	38
52.	—	33	37	31	33	31	—	—	32	—	33
54.	—	25	21	—	27	—	—	—	24	—	27
55.	57	49	53	51	50	49	—	46	47	—	49
62.	—	45	40	—	44	—	—	—	—	—	—
63.	—	40	40	44	43	—	—	38	38	—	42
65.	(121)	—	—	—	—	124	—	—	—	119	—
66.	96	—	95	—	—	96	—	92	92	96	100
69.	29	31	28	—	31	33	25	25	32	—	33
70.	62	63	59	—	65	59	61	62	67	67	71
71.	27	29	28	—	33	35	27	28	30	30	30
72.	—	—	86°	—	90°	—	—	—	—	—	87°
8:1	—	—	81,8	85,5	80,0	85,5	84,4	74,3	—	77,5	82,5
17:1	—	—	80,0	77,9	74,9	—	—	72,7	—	—	—
17:8	—	—	97,8	91,7	93,6	—	—	97,8	—	—	—
9:8	—	—	66,2	64,6	71,4	—	62,3	71,3	—	73,8	68,5
47:45	—	88,3	85,4	—	—	—	—	82,7	—	—	93,0
48:45	—	56,3	56,9	—	—	—	—	48,8	—	—	53,9
52:51	—	82,5	97,4	81,6	82,5	81,6	—	—	—	—	86,8
54:55	—	51,0	39,6	—	54,0	—	—	—	51,1	—	55,1
63:62	—	88,9	100,0	—	97,7	—	—	—	—	—	—
Norma verticalis	Szfen.	—	Pent.	Szfen.	Ovoid	Szfer.	Pent.	Szfen.	Szfen.	Szfen.	Szfen.
Glabella	1	1	1	2	2	1—2	2	1	1	1	2
Prot. occ. ext.	0	—	2	0	0	0	0	0	—	0	0
Fossa canina	2	4	3	1	2	2	—	1	3	3	2
Spina nas. ant.	1	1	2	—	1	—	—	1	1	1	—
Alv. prognathism	2	3	1	—	2	—	—	3	3	3	2
Calculated stature	159	—	—	—	—	—	155	155	—	153	162
Taxon	n—x	—	br(p)	p	a—x	br—x	—	n—x	—	—	br

Table 6. Szekszárd-Palánk, avar period: Females (4)

No. of measurements (MARTIN)	193. 10 428 Ad.	196. 10 439 Sen.	198. 10 440 Ad.	200. 10 431 Sen.	215/B. 11 647 Ad.	230. 11 654 Ad.
1.	170	171	183	168	—	—
1c.	172	166	173	169	—	—
5.	95	—	104	—	—	—
8.	150	148	149	145	—	(144)
9.	99	101	103	98	91	90
17.	127	—	126	—	—	—
20.	111	—	—	—	—	—
32/1-a.	50°	—	—	—	—	—
38.	1409	—	1370	—	—	—
40.	90	—	—	—	—	—
45.	(127)	(139)	135	129	—	126
46.	91	84	—	—	88	92
47.	107	—	—	—	102	107
48.	59	(64)	65	71	64	66
51.	39	38	—	—	44	36
52.	36	33	33	35	37	34
54.	23	25	—	25	24	20
55.	46	49	48	55	48	48
62.	—	—	—	—	44	44
63.	40	—	—	—	41	40
65.	114	—	—	128	116	106
66.	90	—	—	103	(87)	95
69.	30	25	—	29	27	26
70.	61	68	59	65	66	59
71.	28	29	32	31	26	27
72.	88	—	—	—	—	—
8:1	88,2	86,6	81,4	86,3	—	—
17:1	74,7	—	68,8	—	—	—
17:8	84,7	—	84,6	—	—	—
9:8	66,0	68,2	69,1	67,6	—	(62,5)
47:45	84,3	—	—	—	—	84,9
48:45	46,5	—	48,2	55,0	—	52,4
52:51	92,3	86,8	—	—	84,1	94,4
54:55	50,0	51,0	—	45,5	50,0	41,7
63:62	—	—	—	—	93,2	90,9
Norma verticalis	Szfen.	Szfer.	Szfen.	Szfen.	Ell.	Szfen.
Glabella	1	3	2	1	4	1
Prot. occ. ext.	1	1	0	0	3	0
Fossa canina	4	2	3	2	4	3
Spina nas. ant.	4	—	—	—	2	2
Alv. prognathism	2	—	2	2	2	3
Calculated stature	148	156	158	156	156	150
Taxon.	l—a	br—x	br—cr	br	—	a—x

Table 7. Szekszárd—Palánk, avar period: Subadults and infants (1)

No. of measurements (MARTIN)	Measurements and indices	4. 10 214 Juv.	43. 10 234 Inf. II.	63. 10 349 Juv.	67. 10 352 Inf. II.	76. 10 383 Inf. II.	84. 10 360 Inf. II.	101. 10 371 Juv.	129. 10 387 Juv.	160. 10 401 Inf. I.
1.	Glabello-occipital length	172	167	179	175	—	—	177	—	147
5.	Basion-nasion length	97	92	94	98	94	—	95	—	—
8.	Maximum breadth of cranium	134	—	142	136	136	139	133	(146)	136
9.	Minimum frontal breadth	90	91	93	98	94	95	96	98	—
17.	Basion-bregma height	139	128	128	—	122	—	122	—	—
40.	Sup. facial length	96	91	—	93	95	—	88	—	—
45.	Bizygomatic breadth	121	—	121	—	—	116	123	132	—
47.	Total facial height	105	94	108	100	—	—	—	(113)	75
48.	Upper facial height	66	57	64	62	63	61	64	(72)	45
51.	Orbital breadth	37	36	—	37	38	35	35	(38)	32
52.	Orbital height	31	32	36	31	32	33	31	(34)	(28)
54.	Nasal breadth	22	27	22	22	22	28	24	—	18
55.	Nasal height	49	41	46	47	46	47	45	—	34
62.	Palatal length	48	—	—	42	—	—	—	—	—
63.	Palatal breadth	38	—	—	—	—	—	—	—	—
65.	Bicondylar-diameter	110	(103)	114	—	—	—	—	106	87
66.	Bigonial-diameter	85	83	93	—	—	—	—	95	—
69.	Mental height	30	26	30	27	—	—	—	33	20
70.	Ramus height	53	37	58	52	—	—	—	61	40
71.	Ramus breadth	33	37	28	33	—	—	—	30	21
8:1	Cranial index	77,9	—	79,3	77,7	—	—	75,1	—	92,5
17:1	Length-height index	80,8	76,7	71,5	—	—	—	68,9	—	—
17:8	Breadth-height index	103,7	—	90,1	—	89,7	—	91,7	—	—
9:8	Transvers. frontopar. index	67,2	—	65,5	72,1	69,1	68,4	72,2	67,1	64,7
47:45	Facial index	86,8	—	89,3	—	—	—	—	85,6	—
48:45	Upper facial index	54,6	—	52,9	—	—	52,6	52,0	54,6	—
52:51	Orbital index	83,8	88,9	—	83,8	84,2	94,3	88,6	89,5	87,5
54:55	Nasal index	44,9	65,9	47,8	46,8	47,8	59,6	53,3	—	52,9
63:62	Palatal index	79,2	—	—	—	—	—	—	—	—

Table 7. Szekszárd—Palánk, avar period: Subadults and infants (2)

No. of measurements (MARTIN)	164. 10404 Juv.	182. 10420 Inf. I.	186. 10423 Inf. II.	203. 10432 Inf. II.	— 10412 Inf. II.	— 10413 Juv.
1.	177	161	—	156	168	184
5.	—	—	86	84	88	—
8.	143	135	141	132	145	136
9.	101	95	92	92	95	92
17.	—	—	118	125	115	—
40.	—	—	85	82	83	—
45.	126	—	113	106	121	114
47.	114	—	89	85	—	—
48.	66	—	54	49	58	62
51.	38	—	34	36	38	38
52.	32	—	31	30	30	32
54.	25	—	—	24	25	21
55.	47	—	40	35	42	43
62.	47	—	—	—	—	41
63.	40	—	—	—	—	36
65.	122	89	105	—	—	—
66.	103	76	—	—	—	—
69.	30	24	22	24	—	—
70.	67	38	—	50	—	—
71.	33	—	27	25	—	—
8:1	80,8	83,9	—	84,6	86,3	73,9
17:1	—	—	—	80,1	68,5	—
17:8	—	—	83,7	94,7	79,4	—
9:8	70,6	70,4	65,3	69,7	65,5	67,7
47:45	90,5	—	78,8	80,2	—	—
48:45	52,4	—	47,8	46,2	47,9	54,4
52:51	84,2	—	91,2	83,3	78,9	84,2
54:55	53,2	—	—	68,6	59,5	48,8
63:62	85,1	—	—	—	—	87,8

Table 8. Szekszárd—Palánk, avar period: Mesurements of long bones. Males

Grave N°	Inventory N°	Femur				Tibia		Humerus		Radius		Ulna		Calculated stature
		greatest length		length in natural position										
		right	left	right	left	right	left	right	left	right	left	right	left	
(11.)	10 216	—	—	—	—	361	367	323	321	—	—	—	—	165
29.	10 225	510	—	506	—	434	—	373	—	—	—	—	—	—
38.	10 232	—	474	—	469	381	384	—	—	—	—	—	—	170
53.	10 343	457	—	455	—	387	—	323	—	—	—	—	—	168
59.	10 346	477	477	472	474	385	386	—	—	—	—	—	—	171
70.	10 354	466	464	464	—	—	—	—	—	—	—	—	275	169
77.	10 357	—	—	—	—	—	362	—	—	—	—	—	—	165
78.	10 358	455	451	(455)	448	358	—	—	—	—	—	—	—	164
93.	10 365	440	439	438	434	360	361	(319)	—	248	—	—	—	164
99.	10 369	—	473	—	469	368	368	—	—	—	—	—	—	166
104.	10 372	432	436	427	431	—	362	—	—	—	—	—	—	163
106.	10 373	410	408	407	414	326	334	298	301	—	—	279	—	160
110.	10 375	—	—	—	—	372	381	—	—	—	—	—	—	169
112.	10 377	—	460	—	457	382	380	—	335	—	(255)	—	—	170
122.	10 378	458	466	455	461	—	—	—	—	—	—	—	—	168
155.	10 399	450	447	444	441	360	—	—	—	—	—	—	—	166
168.	10 407	481	484	476	478	(382)	—	—	—	—	—	—	—	172
181.	10 419	420	—	419	—	339	—	—	—	—	—	—	—	160
195.	10 429	(464)	—	(462)	—	402	—	—	—	—	—	—	—	173
201.	10 442	466	473	466	472	379	374	336	332	254	254	—	—	169
204.	10 433	420	425	415	419	347	346	—	—	—	—	—	—	161
209.	11 642	—	—	—	—	—	352	—	—	228	232	—	—	162
211.	11 644	—	(451)	—	(451)	393	391	334	328	—	(244)	—	—	176
213.	11 645	—	481	—	480	408	411	362	—	273	—	293	266	169
218.	11 649	—	446	—	443	362	(363)	—	(314)	—	—	—	—	165
222.	11 652	449	452	449	451	393	395	325	324	252	—	270	—	168
225.	11 653	460	467	457	463	381	383	—	—	257	—	273	—	170

Table 9. Szekszárd—Palánk, avar period: Measurements of long bones. Females

Grave N°	Inventory N°	Femur				Tibia		Humerus		Radius		Ulna		Calculated stature
		greatest length		length in natural position										
		right	left	right	left	right	left	right	left	right	left	right	left	
2.	10 213	—	—	—	—	—	—	331	325	—	—	—	—	165
30.	10 226	412	408	409	(403)	336	336	285	285	218	216	—	234	153
32.	10 228	421	425	416	418	—	339	—	—	—	—	—	—	155
33.	10 229	451	451	445	—	375	—	311	—	—	—	—	—	161
37.	10 231	420	—	—	—	—	—	—	—	—	—	—	—	155
44.	10 235	401	401	399	(394)	—	—	—	—	—	—	—	—	151
52.	10 342	408	—	404	—	338	—	—	—	—	—	—	—	153
55.	10 344	—	415	—	407	—	333	—	—	—	—	—	—	154
64.	10 350	437	439	434	434	—	345	(318)	325	230	232	255	256	159
69.	10 353	400	401	396	396	—	—	—	—	—	—	—	—	153
74.	10 356	428	431	426	428	—	357	—	312	—	309	—	255	157
97.	10 367	419	—	417	—	340	338	—	—	—	231	—	—	154
98.	10 368	445	438	(435)	434	360	357	—	—	—	—	—	—	159
125.	10 382	—	393	—	390	—	—	—	—	—	—	—	—	150
134.	10 390	430	432	425	427	354	356	—	314	—	238	—	—	158
137.	10 393	423	421	420	417	—	262	302	298	236	—	259	255	155
146.	10 397	—	—	—	—	—	—	299	—	—	—	—	—	154
149.	10 398	378	—	373	—	305	—	268	268	—	—	—	—	146
166.	10 405	439	441	435	434	—	355	—	—	—	—	—	—	159
3.	10 408	—	—	—	—	326	—	—	—	—	—	—	—	152
180.	10 435	423	417	421	417	—	—	305	290	226	217	—	—	155
183.	10 421	419	419	416	416	—	344	—	301	225	226	—	—	155
184.	10 422	442	442	(432)	436	—	359	(309)	—	245	—	—	—	159
188/1.	10 437	411	—	408	—	323	293	—	—	—	—	—	—	153
192.	10 438	465	470	461	466	—	—	322	315	—	242	—	266	162
193.	10 428	387	389	382	385	—	—	289	—	—	—	—	—	148
196.	10 439	425	—	421	—	341	—	—	—	—	—	452	—	156
197.	10 430	—	—	—	—	332	—	—	—	—	—	—	—	153
198.	10 440	—	437	—	433	—	351	—	—	—	(225)	—	—	158
200.	10 431	430	428	428	426	354	350	300	296	—	(230)	—	—	156
202.	10 443	454	460	450	454	365	367	—	325	244	237	264	—	162
215/b.	10 647	423	428	419	424	359	356	290	292	—	—	—	—	156
217.	11 648	453	450	449	447	—	382	—	(312)	—	—	—	—	161
230.	11 654	385	388	380	380	—	317	289	284	—	217	—	233	150

There is, consequently, also an anthropological difference between the first, as well as the second and third contracted groups of the archaeological investigation. A similar phenomenon can be observed in other cemeteries from the Avar period, as well.

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